TOOTH FORM, GROWTH, AND FUNCTION IN TRIASSIC RHYNCHOSAURS (REPTILIA, DIAPSIDA)

by MICHAEL J. BENTON

ABSTRACT. The rhynchosaurs (Reptilia, Diapsida) were important medium-sized herbivores in the middle to late Triassic (245–208 Ma). They had a remarkable multiple-row dentition with a powerful precision-shear bite. Their teeth had ankylothecodont implantation—that is, the deeply rooted teeth were fused to bone of attachment which could also invade the pulp chambers, but there was no socket. There was no typical reptilian tooth replacement from below. Detailed analyses of two typical rhynchosaurs, *Stenaulorhynchus* (middle Triassic) and *Hyperodapedon* (late Triassic), show that the teeth on each jaw are organized into clear longitudinal Zahnreihen. In each of these Zahnreihen, an ontogenetic series of teeth may be seen clearly from the back to the front of the jaw, ranging from newly ankylosed teeth to fully worn and largely resorbed teeth. The cycle of tooth growth and resorption is controlled by normal jaw growth in which the occlusal area moves back constantly: teeth appear to 'swing' into occlusion at the back and out of occlusion at the front of this area of wear. The multiple-row rhynchosaur dentition effectively 'freezes' ontogeny and it offers important information on vertebrate tooth replacement, especially in view of the fact that the fossil material offers excellent histological detail.

RHYNCHOSAURS, a group of small- to medium-sized reptiles of the Triassic Period (245–208 Ma), have aroused considerable interest recently because of their problematic relationships, their debated ecological role, and the remarkable anatomy of their skulls and teeth. Rhynchosaurs have classically been grouped with the living tuatara *Sphenodon* in the Order Rhynchocephalia of the Class Lepidosauria (e.g. Romer 1966; Kuhn 1969), whereas anatomical evidence strongly suggests a position close to the archosaurs (Hughes 1968; Cruickshank 1972; Benton 1983*b*, 1984). Rhynchosaurs were dominant in several faunas of the middle and late Triassic, and they became extinct just before the radiation of the dinosaurs at the end of the Triassic. It has been suggested that rhynchosaurs ate plants (Huene 1939; Romer 1963; Sill 1971*a*, *b*; Benton 1983*a*, *b*) or molluscs (Burckhardt 1900; Chatterjee 1969, 1974, 1980).

The teeth of rhynchosaurs are not acrodont, as has been stated (e.g. Romer 1956, p. 450; Edmund 1969, p. 153), but deeply rooted and firmly fixed with bone of attachment (ankylothecodont: Chatterjee 1974). The most remarkable feature of the teeth is that they were not replaced in a typical reptilian way, but continued to grow throughout their functional life.

The aims of this paper are to describe the morphology, histology, and growth of the teeth in two rhynchosaurs, *Hyperodapedon* from the late Triassic of Elgin, north-east Scotland, and *Stenaulorhynchus* from the middle Triassic of the Songea district, southern Tanzania; to discuss the functions and adaptations of the peculiar rhynchosaur dentition; and to consider the evolution of such a dentition.

Repository abbreviations used are: BM(NH), British Museum (Natural History); CUMZ, Cambridge University Museum of Zoology; NUGD, Newcastle University, Geology Department. Additional figures showing tracings of the serial sections have been deposited with the British Library, Boston Spa, Yorkshire, U.K., as Supplementary Publication No. SUP 14023 (7 pages).

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MATERIALS AND METHODS

Rhynchosaur teeth and jaws

Tooth-bearing elements are the most commonly found remains of rhynchosaurs in many locations, and several accounts of the general morphology of the dentition have been given (e.g. Huxley 1869; Lydekker 1885; Huene 1938; Sill 1971*b*; Chatterjee 1974). The last two authors gave some histological information also. The anatomy of the maxilla and dentary suggests that true rhynchosaurs fall into two natural groups: those of the middle Triassic (*Stenaulorhynchus* from Tanzania, *Mesodapedon* from India, and *Rhynchosaurus* from England), and those of the late Triassic (*Hyperodapedon gordoni* from Scotland, *H. huxleyi* ('*Paradapedon*') from India, *Scaphonyx fischeri* from Brazil, *S. sanjuanensis* from Argentina, '*Supradapedon*' from Tanzania, as well as some unnamed forms from Nova Scotia and Texas). In the present study, tooth-bearing elements of *H. gordoni* and *Stenaulorhynchus* were sectioned in several ways in order to provide further information on the late Triassic forms and new information on one of the earliest known rhynchosaurs. A selection of sectioning techniques was necessary because of the complexity of the arrangement of the teeth—normal methods of preparation by the removal of matrix and outer bone layers would have yielded little information.

H. gordoni is represented by about thirty-five individuals from the Lossiemouth Sandstone Formation (early Norian?) of Lossiemouth East and West Quarries (Nat. Grid Ref. NJ 236707, NJ 231704) and Spynie Quarries (NJ 219656, NJ 223657). The remains include most portions of the skeleton and skull, and detailed restorations have been possible (Benton 1983*b*). *Hyperodapedon* was a squat, 1·3 m long quadruped with powerful hindlimbs that could have been used for scratch-digging (text-fig. 1*a*). The skull was specialized, with a broad posterior portion to accommodate powerful jaw adductor muscles (text-fig. 1*b*). The upper dentition is borne on two maxillary tooth-plates, each of which has several rows of teeth and is bisected by a deep longitudinal groove. The lower jaw fits snugly into this groove when the jaws are shut, and this can be likened to the blade of a penknife fitting into its handle (Huxley 1869). There are toothless beak-like premaxillae at the front of the skull, and the lower jaws curve up on either side to a high pointed rostrum (text-fig. 1*c*). The quadrate-articular jaw articulation permitted no antero-posterior sliding, and patterns of tooth wear confirm that *Hyperodapedon* had a powerful precision-shear bite (Benton 1983*b*) rather than a cutting-sawing movement as suggested in *Scaphonyx* by Sill (1971*b*). There are two series of teeth in the lower jaw (text-fig. 1*d*, *e*). Along the dorsal margin of the dentary is a palisade of tightly packed buccal teeth with no intervening bone and lower down, on the medial surface of the dentary, is a series of broader lingual teeth.

Stenaulorhynchus stockleyi Haughton 1932 is represented by remains of fifty to fifty-five individuals (Huene 1938, A. R. I. Cruickshank, pers. comm.) from the Manda Formation (early Anisian?) of the Songea district, southern Tanzania. Specific localities include the region of the Litumba to Songea road, west of Njalila and west of Mkongoleko (Attridge/Charig/Cox field notes, BM(NH); Parrington field notes, CUMZ). *Stenaulorhynchus* was about 1·6 m long, and very like *Hyperodapedon* in general appearance. However, the skull shows less of the advanced rhynchosaur characters (Huene 1938, pl. 1, 2). It is lower and less broad at the back, and the eye faces more

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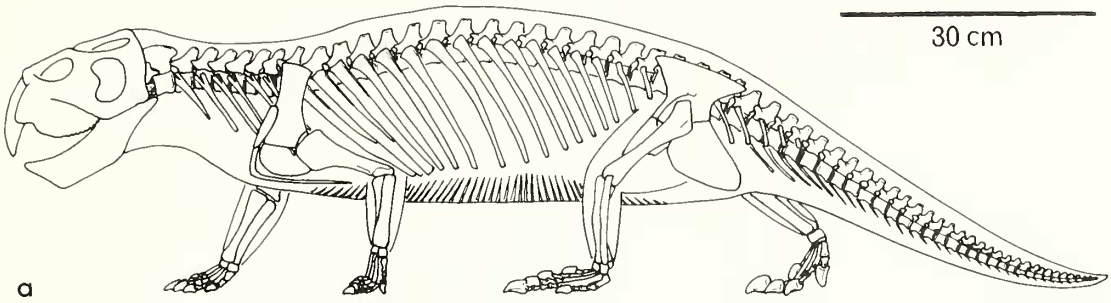
TEXT-FIG. 1 (*opposite*). The rhynchosaur *Hyperodapedon gordoni* from the Lossiemouth Sandstone Formation of Elgin, north-east Scotland: *a*, lateral view of the skeleton in walking pose; *b*, ventral view of the skull, showing the maxillary tooth-plates; *c*, lateral view of the skull with the lower jaw in place; *d*, medial view of the lower jaw showing the two distinct tooth rows on the dentary; *e*, diagrammatic cross-section through the lower jaw and maxilla to show occlusal relationships of the teeth. Abbreviations: an, angular; art, articular; bt, buccal teeth; d, dentary; ec, ectopterygoid; lt, lingual teeth; mx, maxilla; pm, premaxilla; pra, prearticular; q, quadrate; sa, surangular; sp, splenial.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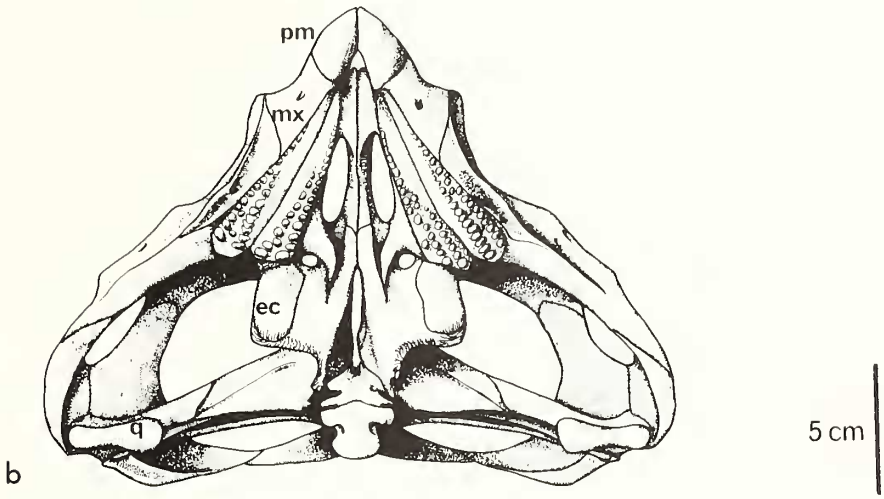
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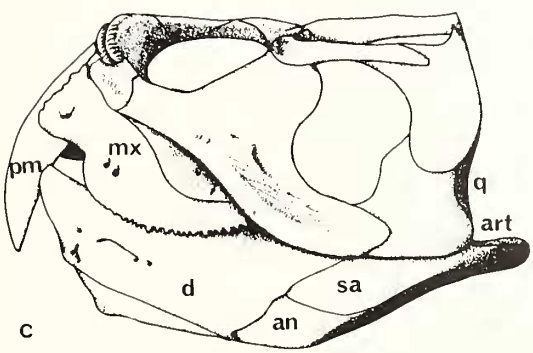
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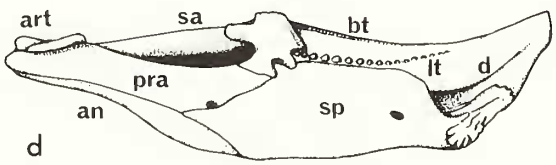
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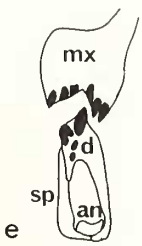
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sideways, and the braincase is placed further forward. The arrangement of the dentition of the maxillary tooth-plate and of the dentary is rather different from that of *Hyperodapedon*. The maxilla bears one large longitudinal row of teeth laterally and two or more further rows of smaller teeth in the middle and medial portions of the tooth-plate, on the occlusal and lingual surfaces. The dentary is rather flat-topped and bears several rows of teeth that pass from the occlusal to the lingual surface. In both cases, it is hard to distinguish which teeth should be termed buccal and which lingual.

Specimens examined

Hyperodapedon gordoni Huxley 1859

BM(NH) R3140. Partial skull; Lossiemouth (E).
BM(NH) R4780. Left dentary; Lossiemouth (E).
EM 1926. 6. Left maxilla; Lossiemouth (E)?
NUGD A. Partial skull; Spynie.
NUGD B. Skull; Spynie.

Stenaulorhynchus stockleyi Haughton 1932

BM(NH) R9271. Partial right dentary; Songea district, southern Tanzania.
BM(NH) R9272. Right maxilla.
BM(NH) R9273. Left dentary.
BM(NH) R9274. Right dentary.
BM(NH) R9275. Left maxilla.
BM(NH) R9276, R9277. Right maxilla (cut into two pieces).
BM(NH) R9278. Maxilla.
BM(NH) R9279. Juvenile left maxilla.
BM(NH) R9280. Right maxilla.
BM(NH) R9281. Right maxilla.
BM(NH) R10007. Partial right dentary.
BM(NH) R10008. Partial right maxilla.
CUMZ T992. Right maxilla.
CUMZ T993. Juvenile left maxilla.
CUMZ T1112 (FRP 2). Right lower jaw, lacking splenial (on loan to the BM(NH)).
CUMZ T1138. Right maxilla.

Serial grinding and thin sectioning

In the course of the present study, the morphology and arrangment of the maxillary and dentary teeth of all available material of *Hyperodapedon* was studied (Benton 1983*b*). Some general information on the teeth of *Stenaulorhynchus* has been presented (Huene 1938; Chatterjee 1980) and further details, based on an examination of the specimens preserved in the BM(NH) and CUMZ are given below. Two methods were employed in order to study the internal arrangement and histology of the teeth: serial grinding and peeling, and standard thin sectioning.

The serial grinding and peeling technique used was similar to that employed in studies of the internal structure of invertebrate fossils such as brachiopods and corals and in studies of calcareous sediments (e.g. Ager 1965; Allman and Lawrence, 1972). A piece of tooth-bearing bone was selected that appeared to be well preserved internally, and yet was broken, or otherwise damaged and of little use in studies of its external form. The procedure was as follows:

1. Mount the specimen in the desired orientation in a cold-setting compound (e.g. polyester resin, or other embedding resin) and attach this to the serial grinder base plate.
2. Grind first flat surface.
3. Remove specimen from grinder and polish flat surface with progressively finer grades of moistened carborundum powder, to grade 600 or 1000, on a glass plate.
4. Wash the polished surface and dry. Do not touch the cleaned surface.
5. Etch by holding polished surface of specimen in a tray of 5% hydrochloric acid for 20 seconds in order to heighten non-calcareous features.

6. Neutralize the acid and wash with distilled water.
7. Dry by slight heating or with acetone.
8. Mount specimen in a sand box or in plasticene, if necessary, so that etched surface faces up and is horizontal.
9. Cut a piece of acetate film to allow at least 1 cm all round the specimen.
10. Flood etched surface of specimen with acetone (not too much).
11. Hold acetate film in U-shape and apply carefully from the centre outwards in order to exclude gas bubbles. This must be done smoothly without touching the film or moving it around.
12. Allow five minutes or more for the acetate film to harden and remove by peeling back from one corner.
13. Trim the acetate film to the edge of the impression, and mount it immediately between two microscope slides. Tape these together on the long edges.
14. Return specimen to serial grinder in exactly the original orientation, advance by 0·1 or 0·5 mm, and repeat steps 2–14.

This technique produced good results for materials of both *Hyperodapedon* and *Stenaulorhynchus*. The bone of *Hyperodapedon* is normally preserved very poorly and is so soft that positive preparation is very difficult. The natural rock moulds were of high fidelity and casts of bones were made using flexible synthetic rubber compounds (Benton and Walker 1981). The bone is still in the form of apatite and occasionally it has been infiltrated with iron oxide minerals (e.g. goethite) which fill all vessel canals and cracks. A lower jaw of *Hyperodapedon* (NUGD B) was retrieved and sectioned in three planes: vertical transverse, vertical longitudinal, and horizontal. On ground surfaces and on peels, bone was white, dentine yellow, enamel translucent, and the infilled cavities steely blue (unweathered) or reddish brown (weathered). Unfortunately, no suitable maxilla of *Hyperodapedon* could be found for serial sectioning. In *Stenaulorhynchus* the bone is preserved as apatite with good detail of the original structures. It is usually hard, the cavities are infilled with iron oxide minerals, and the surface is often badly cracked. Isolated fragments of maxilla and dentary (BM(NH) R10007, R10008) were sectioned in the vertical longitudinal and vertical transverse planes respectively. In section, bone is white, dentine cream-coloured, enamel translucent, and the infilled cavities steely blue (unweathered) or reddish brown (weathered).

The peels were then used in two ways: (1) to reconstruct the jaw and teeth in three dimensions, and (2) to study microscopic detail.

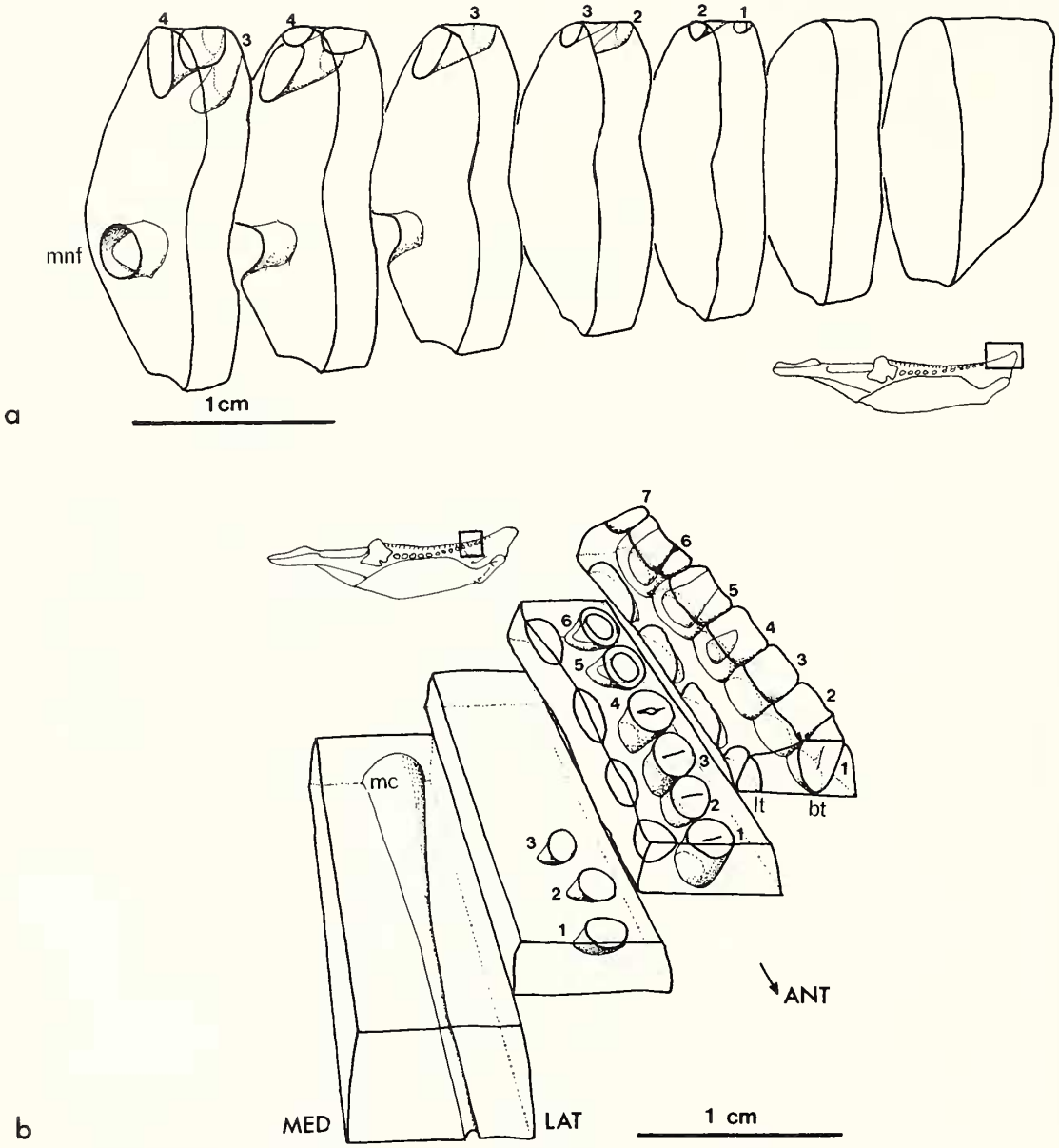
1. Three-dimensional reconstruction. A tracing was made of each peel using an ordinary photographic enlarger, and these were arranged in sequence. Copies were made on to glass plates with an indelible pen. The enlargement here was calculated so that it matched the scaling-up factor given by the ratio,

$$\frac{\text{thickness of glass plate}}{\text{original peel spacing.}}$$

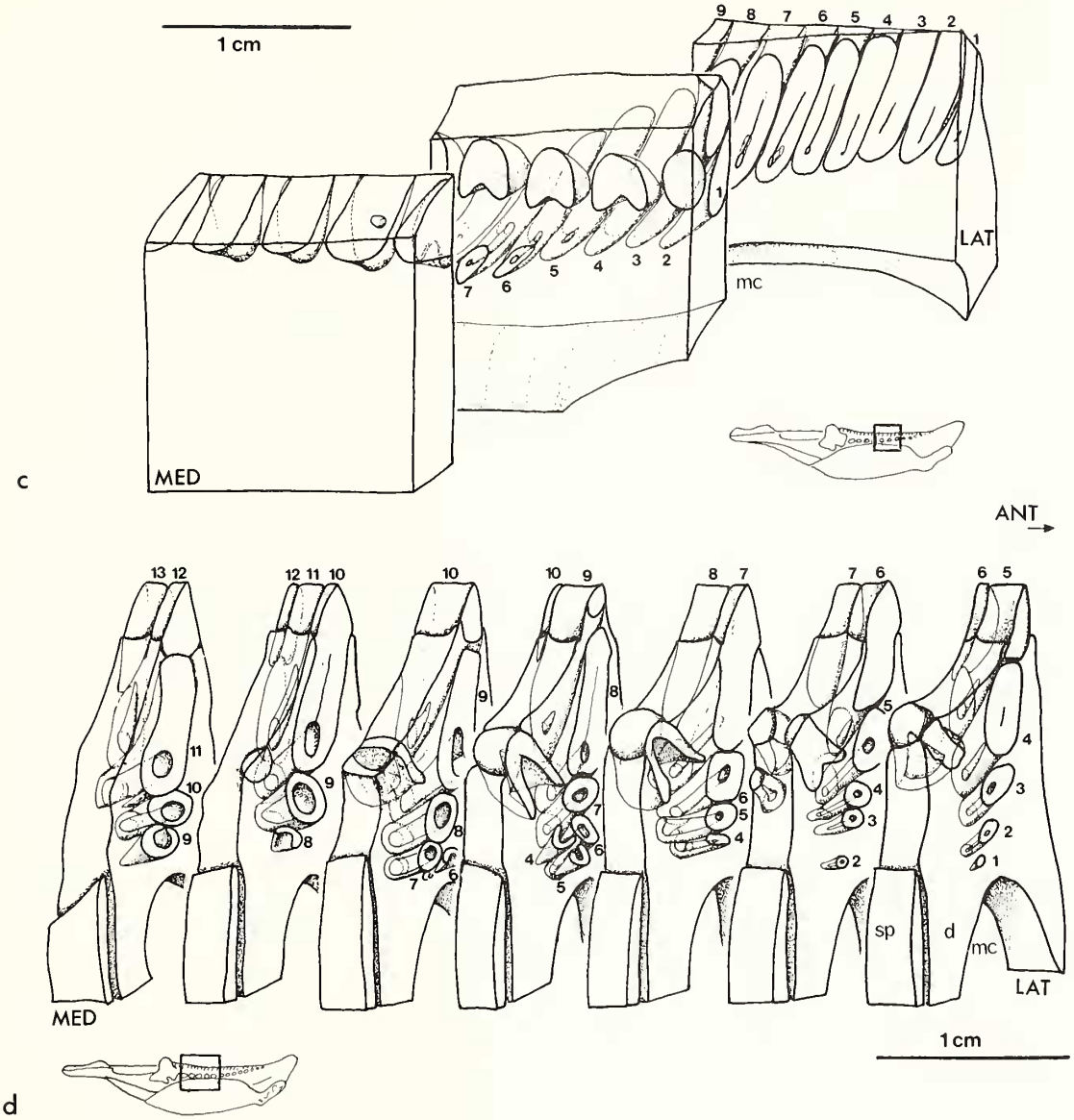
Bundles of five or so glass plates were bound together with clear tape so that the tracings on each were in register. These bundles were drawn as block diagrams to give a three-dimensional reconstruction of the arrangement of the teeth (text-figs. 2, 7, 8).

2. Microscopic detail. Individual peels were examined under an ordinary light microscope in order to elucidate histological details of the bone and teeth. Tracings were made using an ordinary photographic enlarger or a microscope with a drawing attachment. Photographs were also taken through a microscope.

Normal thin sections were made from some pieces of jaw, ground to a thickness of 30 μ, the standard for geological material. These preserved colours better than the peels, and they were used for higher magnification drawings and photographs, and for examination under cross-polarized light. Nevertheless, the peels also preserved fine detail and produced extremely good photographs (e.g. Pls. 67, 68).



TEXT-FIG. 2. Graphic reconstructions of the dentition of the left lower jaw of *Hyperodapedon gordoni* (NUGD B). Drawn from serial sections taken at 0·5 mm spacing, and traced on to glass plates at a magnification of 10 ×. The block diagrams are drawn in different orientations: *a*, anterior part of the dentary; *b*, anterior middle part of the dentary; *c*, middle part of the dentary; *d*, posterior part of the dentary. The location of each block diagram is indicated on an outline lower jaw. Teeth are numbered from front to rear in each view. Abbreviations: ANT, anterior; bt, buccal teeth; d, dentary; LAT, lateral; lt, lingual teeth; mc, Meckel's canal; MED, medial; mnf, mandibular foramen; sp, splenial.



THE DENTITION OF *HYPERODAPEDON*

Arrangement of teeth in the maxilla

The teeth on either side of the central groove in the maxillary tooth-plate are arranged in approximately longitudinal and diagonal rows (text-fig. 1*b*; Pl. 66, fig. 1). Most specimens show a medial field with three or four longitudinal rows that is wider than the lateral field with two or three rows. At the front of the tooth-plate, usually only one row of teeth is to be seen, which is partly because of wear by the dentary teeth and dentary bone. Further back, additional longitudinal rows of teeth appear at the sides of the groove. Very large old specimens of *Hyperodapedon gordoni* are not

known, but they may have added supplementary rows up to a total of six or seven at the back of the tooth-plate, as in *H. huxleyi* and *Scaphonyx fischeri* (Lydekker 1885; Huene 1942; Chatterjee 1974, 1980). Some longitudinal rows show regular packing of teeth while others are irregular, and occasional stray teeth may occur at the edge of the tooth-plate (Benton 1983*b*, fig. 15). The row on the lateral side of the groove is regular and consists of triangular pyramidal teeth, with the longest flat plane facing forwards (Pl. 66, fig. 1). The other rows consist of conical teeth which are less regular in shape. In vertical section, the teeth are directed at right angles to the surface of the curved maxillary tooth-plate.

Arrangement of teeth in the dentary

Three-dimensional reconstructions, made in different planes, from a sequence of vertical transverse sections through the top of the lower jaw show the patterns of teeth in different parts of the jaw (text-fig. 2).

Teeth are virtually absent, or very small, near the front of the dentary, and they increase in length backwards until the roots are just above the meckelian canal at the back. The buccal teeth are tightly packed with very little intervening bone dorsally, and the exposed portion is flattened medio-laterally by tooth wear. They are deeply rooted cylindrical teeth that curve gently up, forwards, and laterally. The great variability in the pulp cavity may be seen in all sections.

The lingual teeth are regular in arrangement and occur in a single spaced row, although occasional extra teeth appear beneath the row (text-fig. 2*d*; Pl. 66, fig. 2). The lingual teeth are pyramid-shaped, superficially rather like the maxillary teeth, but they are clearly more thimble-shaped when seen in section (text-fig. 2*d*). They are spaced differently from the buccal teeth (five lingual to nine buccal teeth longitudinally).

Jaw occlusion and tooth wear

Clear indications of tooth wear have been observed in *Hyperodapedon* (Benton 1983*b*). In summary, the middle portion of the tooth-bearing area of both maxilla and dentary is worn. The teeth and surrounding bone that come into contact are flattened.

The curvature of the maxillary tooth-plate is greater than that of the dentary (text-fig. 1*c*) so that when the jaws close only the middle portions come into contact. Arc-shaped areas are worn flat on the medial and lateral sides of the dentary, and these exactly match the areas of wear on the maxilla (text-fig. 1*b*). The buccal teeth of the dentary bite against the bone in the groove, but lingual dentary teeth occasionally directly meet maxillary teeth (text-fig. 1*e*). When lingual teeth bite against bone of the maxilla, shallow pits may be left, which strongly indicates that *Hyperodapedon* had a precision-shear bite (Benton 1983*b*), as seen in the lizard *Uromastix* (Robinson 1976), rather than the propalinal sawing type of *Sphenodon* which was suggested by Sill (1971*b*) for *Scaphonyx*.

The newest teeth at the back of the jaws are not in occlusion, and are thus unworn. The oldest teeth at the front of the jaws are generally heavily worn. This wear must have occurred in juvenile stages,

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EXPLANATION OF PLATE 66

The dentition of *Hyperodapedon gordoni*.

Fig. 1. Occlusal view of a left maxillary tooth-plate, BM(NH) R3140; × 1·5.

Fig. 2. Transverse vertical section through the top of the dentary, showing the 'waisted' shape of the buccal tooth just below the occlusal margin, the roots of adjacent buccal teeth in cross-section, and a supernumerary lingual tooth (left), × 8.

Fig. 3. Transverse vertical section of a dentary buccal tooth, showing the typical wear shape; medial is to the left; this section is located in text-fig. 3*c*, × 15.

Fig. 4. Transverse vertical section through the anterior part of the dentary, showing a heavily worn and resorbed tooth, and the 'track' of disturbed bone below it, × 5.

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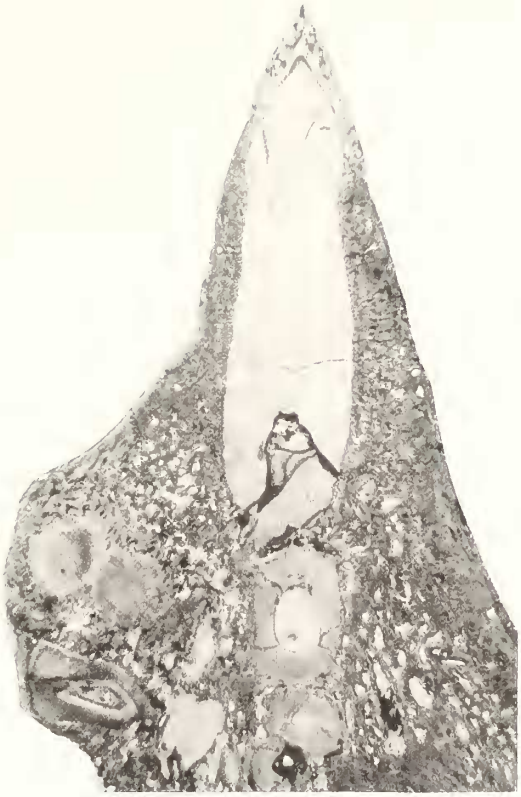

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BENTON, rhynchosaur dentitions

since these teeth do not occlude in the adult. Relative growth causes the maxilla to curve upwards away from the dentary, and progressively more posterior portions of the tooth rows come into occlusion. It should be noted that the degree of tooth wear is not related to skull size, but probably depends on the individual's diet as in *Sphenodon* (Robinson 1976).

Tooth form

In general, the teeth of *Hyperodapedon* are deeply fixed in the bone of the jaw and they have open roots with pulp cavities of varying size. The bulk of the tooth is composed of dentine, and enamel may be seen capping the upper portion in some cases.

The maxillary teeth have short roots and shallow conical pulp cavities. They may be nearly circular in cross-section with a central root canal. In microscopic sections they show occasional longitudinal fluting on the surface, and radial dentinal tubules (Pl. 67, fig. 4). These features have been described in detail in *H. huxleyi* by Chatterjee (1974, pp. 228–229).

More information is available on the dentary teeth of *Hyperodapedon*. A series of vertical transverse sections (text-fig. 3) shows the form and emplacement of the teeth and variation in their pattern along the jaw. Anterior portions (text-fig. 3*a*) lack teeth, probably as a result of wear and migration of the teeth occlusally, or the teeth are small and the roots closed (text-fig. 3*b*; Pl. 66, fig. 4). Further back, a series of buccal teeth is seen in every section. This is not a succession of teeth or a Zahnreihe. The buccal teeth slope forwards, laterally, and upwards, so that most of them are cut obliquely in vertical sections. Each tooth is waisted at about the mid point which is shown by unworn crowns (text-fig. 3; Pl. 66, fig. 2). Wear on the inner surface produces a medial concavity and the outer surface retains its original convex profile (Pl. 66, fig. 3). At the base, most buccal teeth display an axial pulp cavity that may be relatively large or small in an apparently random way and it is not dependent on the level of the section (text-fig. 3*c–e*). Vertical longitudinal sections through the dentary show the curved shape of the buccal teeth (text-fig. 4*b–d*), and horizontal sections (text-fig. 5*a–c*) show that they are nearly circular in section, rather than compressed, as suggested by Chatterjee (1974, p. 230) for *H. huxleyi*, except when they are worn to a knife-like edge on the top of the jaw (text-fig. 5*c*).

The lingual teeth are shorter and shaped like thick-walled thimbles. Because they are directed medio-dorsally, the standard sectioning planes do not cut them axially, but these teeth were clearly cylindrical with a deep and narrow conical pulp cavity (text-figs. 3*c*, *d*, 4*a*, *b*, 5*b*).

Bone and tooth histology

The serial peels and microscopic sections from the lower jaw of *Hyperodapedon* reveal a great deal of detail concerning the histology of the bone and teeth. The bone may be divided into three types:

1. Laminar fibrolamellar with parallel longitudinal primary osteons: in regions with teeth (Pl. 66, figs. 2–4; Pl. 67, figs. 1, 2, 4). The osteons are occluded to a greater extent towards the edge of the jaws

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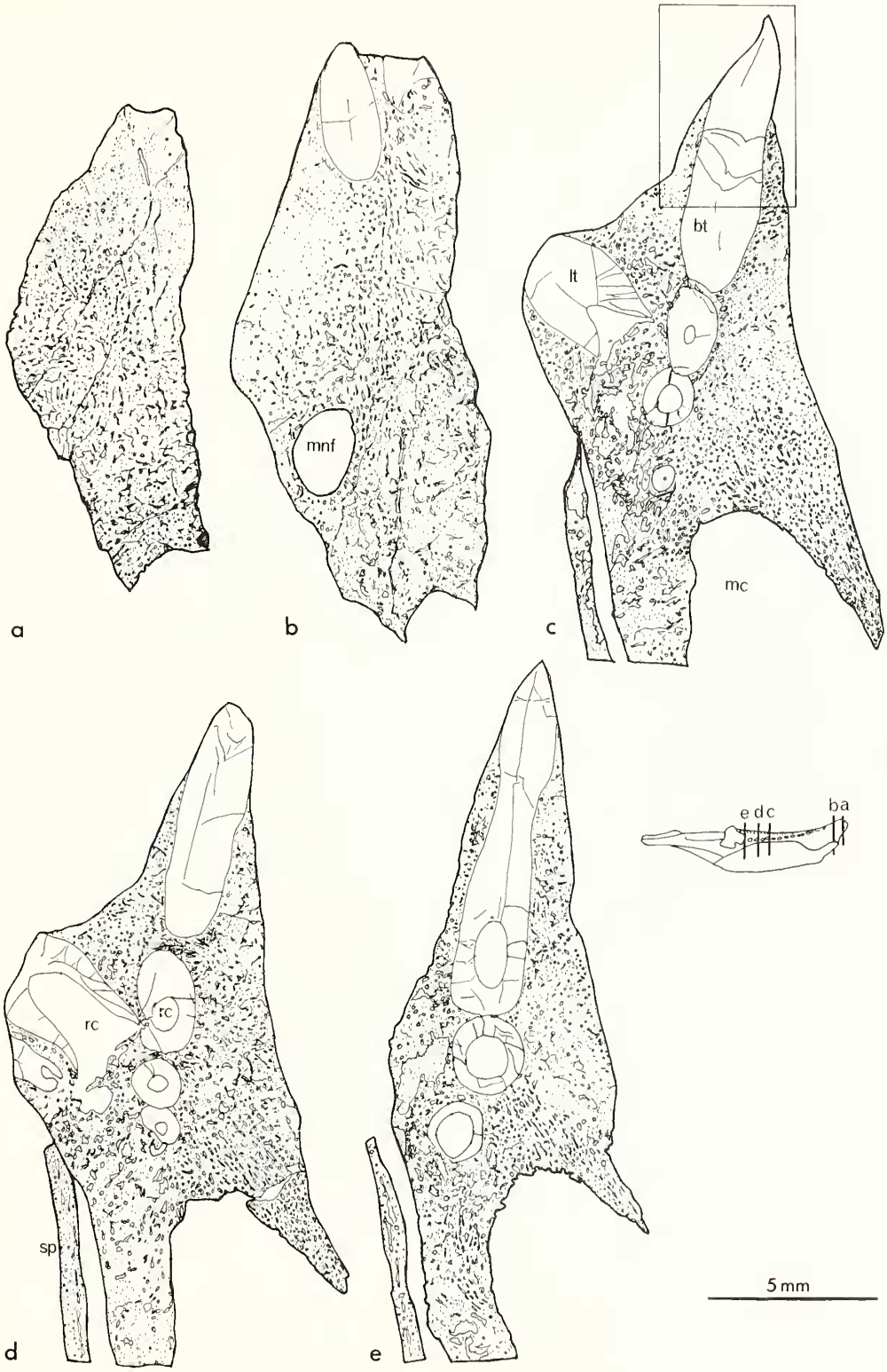
TEXT-FIG. 3 (*opposite*). Transverse vertical sections of the upper part of the mandible of *Hyperodapedon gordoni* (NUGD B) showing buccal and lingual teeth. The locations of the sections are indicated on an outline mandible. *a*, anterior mandible; teeth are absent. *b*, anterior mandible, further back; heavily worn teeth with closed roots, and a large vessel canal. *c*, mid-jaw; a heavily worn lingual tooth and a series of buccal teeth sectioned at different positions along their length. The upper one shows a characteristic wear shape; the lower ones show open roots near the apex. These are not successional teeth, but sections at an angle through teeth that slope up and forwards, and all are functional. The area shown in Pl. 66, fig. 3 is outlined. *d*, further back; a rare abnormality where a small additional lingual tooth occurs, and erosion of a buccal tooth by the growth of a lingual tooth is also seen. *e*, posterior part of dentary, behind the lingual tooth row; a series of sections of buccal teeth with broad root canals and the characteristic 'waisted' appearance of the barely erupted dorsal tooth. Abbreviations: bt, buccal teeth; lt, lingual teeth; mc, Meckel's canal; mnf, mandibular foramen; sp, splenial.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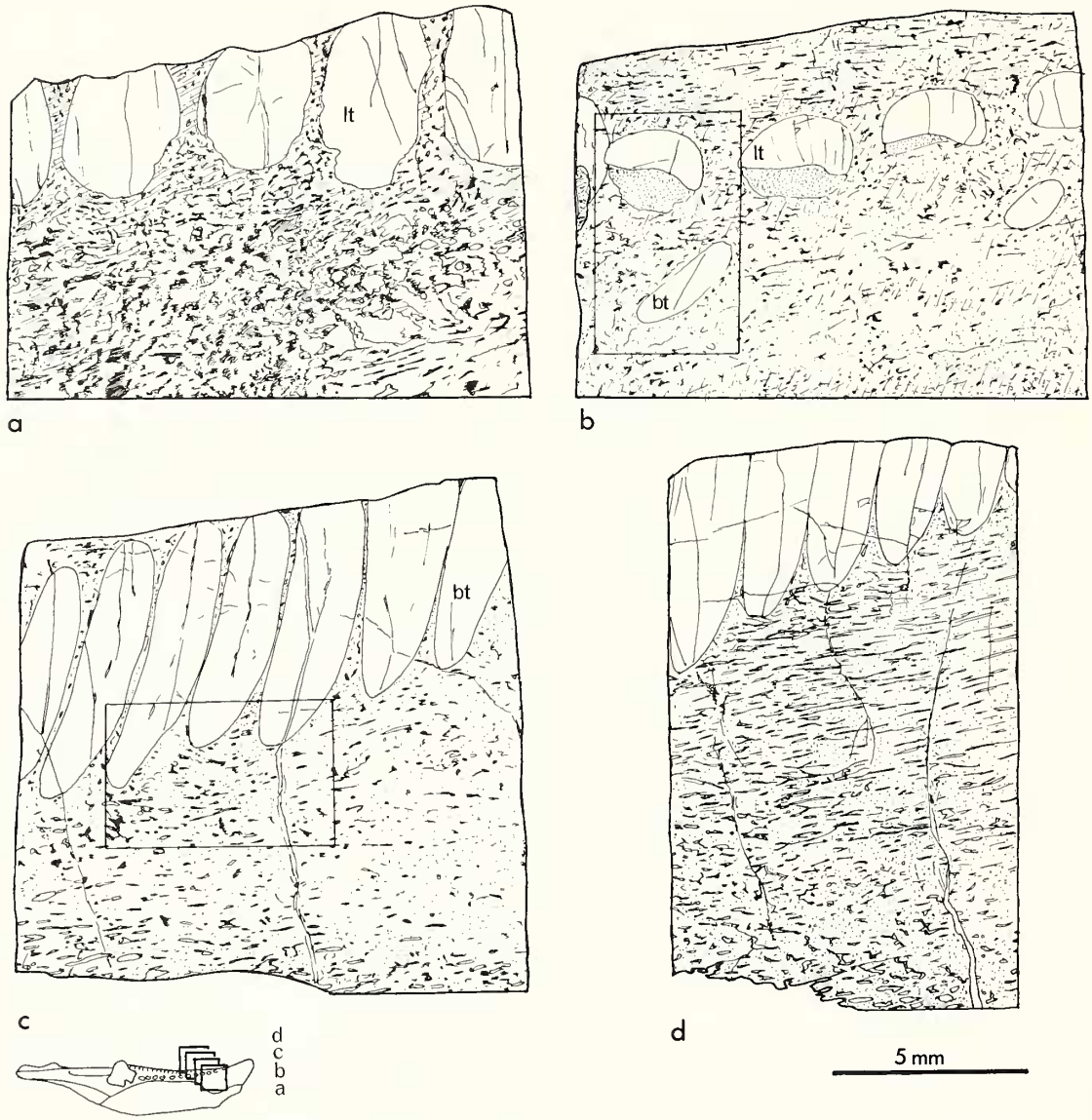


TEXT-FIG. 4. Longitudinal vertical sections of the upper part of the mandible of *Hyperodapedon gordoni* (NUGD B), showing the buccal and lingual teeth. The locations of the sections are indicated on an outline mandible. *a*, medially located section; lingual teeth only are seen. *b*, slightly more laterally; the lingual teeth are much reduced and the roots of the buccal teeth appear, indicating that they slope up, forwards, and laterally. The area shown in Pl. 67, fig. 3 is outlined. *c*, more laterally; the full shape of longitudinal sections through the closely packed buccal teeth is clear. The area shown in Pl. 67, fig. 4 is outlined. *d*, towards the lateral margin of the jaw; only partial oblique sections through buccal teeth appear, and show their very close packing. Abbreviations: bt, buccal teeth; lt, lingual teeth.

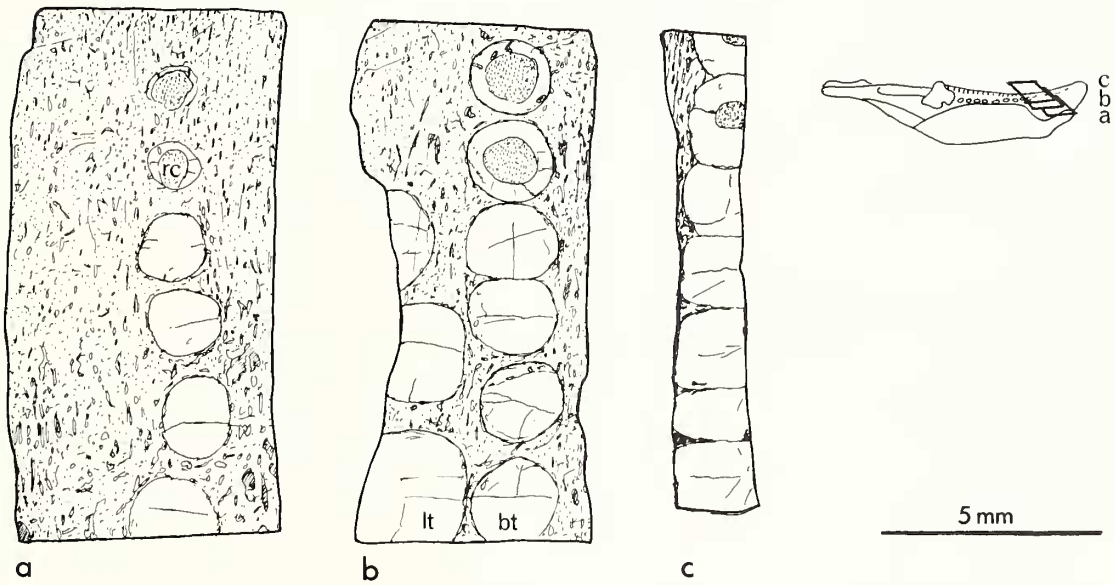
and on either side of the teeth where the bone itself may be subject to wear. This may be functionally equivalent in part to the highly calcified layer of bone observed on the sides of the jaw of *Sphenodon* by Harrison (1901, pp. 200–201). Further forwards in the jaw, where the teeth are older and they have closed root canals, the bone becomes almost wholly compact in the vicinity of the teeth (text-fig. 3*a*, *b*; Pl. 66, fig. 4).

2. Recticular (cancellous) fibrolamellar: in the centre of bones and away from the teeth (text-figs. 3, 4; Pl. 66, figs. 2, 4).

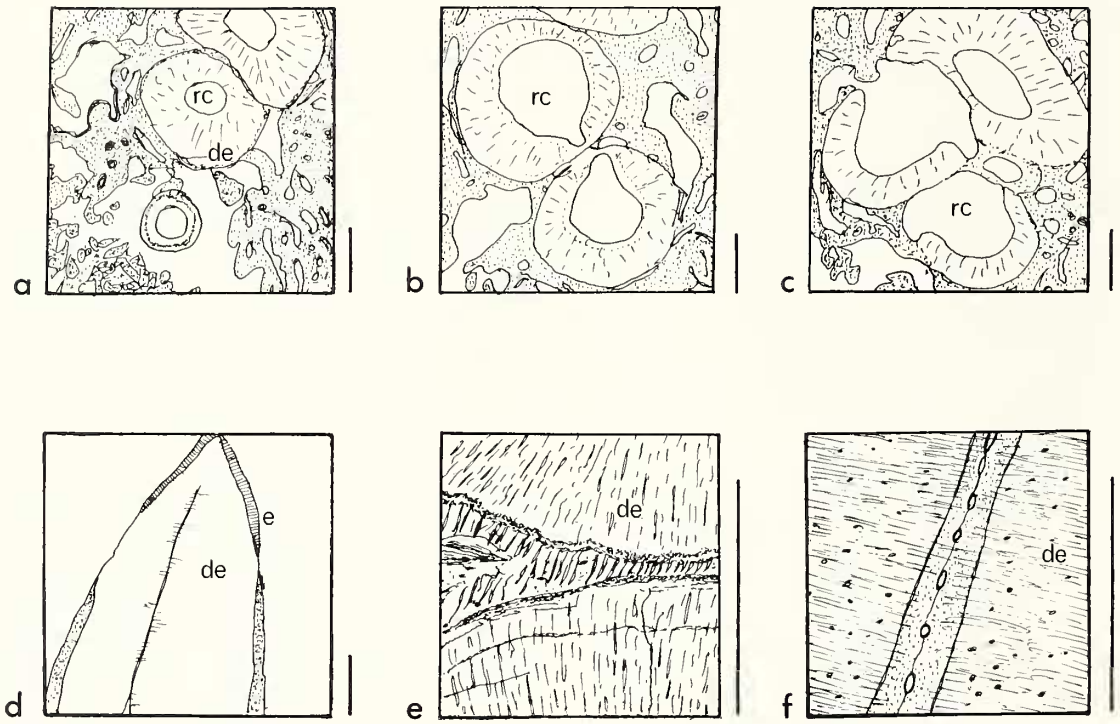
3. Bone of attachment: around the sides of the teeth, the bone is remodelled and takes on a regular appearance with tightly packed small osteons (Pl. 66, figs. 2, 3; Pl. 67, fig. 3). These may have a compressed appearance when they occur between two closely spaced teeth (Pl. 67, figs. 4, 6). At the base of the growing teeth the bone is highly vascular (e.g. text-fig. 6*a–c*; Pl. 66, fig. 2; Pl. 67, figs. 2, 3, 4), and this is particularly marked in posterior parts of the jaw. In the front of the jaw, a track of extensively remodelled bone may be seen at the base of certain teeth (Pl. 66, fig. 4)—this probably marks the passage of the tooth through the bone during jaw growth when the tooth was maintaining its position in occlusion. The remodelled bone may also indicate resorption of a tooth that is no longer in occlusion.

In micrographs of the *Hyperodapedon* jaw (e.g. Pl. 67, fig. 6), osteocyte lacunae are clearly visible in the bone matrix. In some cases there appear to be transverse fibres that run from one tooth to the next (text-fig. 6*e*). These may be traces of collagen fibre directions, or they may be preservational artefacts.

Enamel is not always present on the dentary teeth, but it may be represented by some white, radially prismatic, deposits (text-fig. 6*d*). Enamel is probably present initially on the tooth crowns and is later worn off, rather than being totally absent as suggested by Sill (1971*b*) for *Scaphonyx*. In



TEXT-FIG. 5. Horizontal sections of the upper part of the mandible of *Hyperodapedon gordoni* (NUGD B) showing the buccal and lingual teeth. The locations of the sections are indicated on an outline mandible. *a*, ventrally placed section; only the roots of some buccal teeth are seen, some with open root canals. *b*, higher up; both lingual and buccal teeth appear, and the latter can be seen to be more closely packed than the former. *c*, section near the occlusal margin of the dentary; the worn, closely packed buccal teeth occupy nearly the whole width of the jaw. Abbreviations: bt, buccal teeth; lt, lingual teeth; rc, root canal.



TEXT-FIG. 6. Sections of dentary teeth of *Hyperodapedon gordoni* (NUGD B). Scale bars all measure 0·5 mm. *a–c*, transverse sections of buccal teeth near the root apices, showing open root canals and some erosion of tooth material by neighbouring teeth; *d*, transverse vertical section through the upper part of a buccal tooth, showing a thin enamel cap with perpendicular prismatic fabric; *e*, detail of the compact bone between two buccal teeth in horizontal section, showing the diffuse tooth margin and 'fibres' in the bone perpendicular to the tooth surface; *f*, detail of the bone between two buccal teeth in vertical section, showing the closely packed primary osteons and the dentinal tubules. Abbreviations: de, dentine: e, enamel; rc, root canal.

EXPLANATION OF PLATE 67

Histology of the bone and teeth of the dentary of *Hyperodapedon gordoni*. Sections from NUGD B.

Fig. 1. Horizontal section taken above Meckel's canal, showing laminar fibrolamellar bone with largely occluded canals, × 30.

Fig. 2. Horizontal section taken at the root apex of a buccal tooth, showing compact laminar fibrolamellar bone, and some bone of attachment, × 30.

Fig. 3. Longitudinal vertical section taken towards the medial side of the dentary, showing part of a lingual tooth with open root canal and loose bone at the base (top), and the lower part of a buccal tooth; the shiny mineral that infills the cavities is goethite; this section is located in text-fig. 5*b*, × 13.

Fig. 4. Longitudinal vertical section through the bases of four buccal teeth showing the laminar fibrolamellar bone, and the diffuse tooth/bone of attachment margin; this section is located in text-fig. 4*c*, × 13.

Fig. 5. Transverse vertical section through the roots of some buccal teeth and a lingual tooth, showing erosion of the former by the latter; the erosion occurs along a typical arcuate front, × 12.

Fig. 6. Horizontal section through two buccal dentary teeth, showing the margins of two teeth with clear radial dentinal tubules, and the close-packed bone of attachment between the teeth, × 80.

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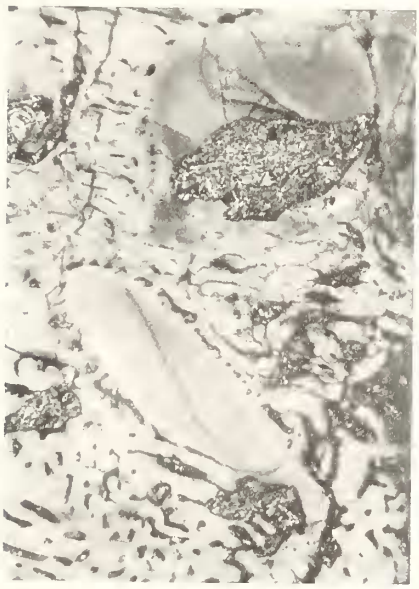

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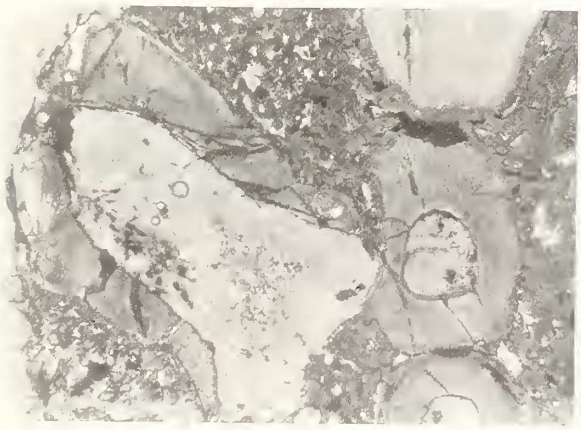

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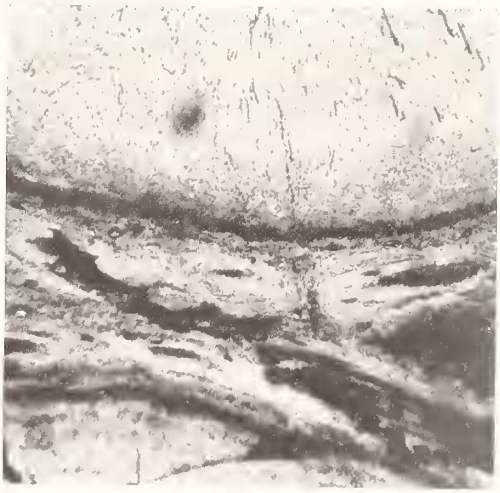


6

BENTON, rhynchosaur dentitions

Hyperodapedon, the bulk of the tooth is composed of orange-yellow orthodentine which clearly shows radial dentinal tubules in microscopic section (Pl. 67, fig. 6), and these are picked out by the iron oxide infill of the pulp cavity on etched polished surfaces. The tubules run from the pulp cavity to a diffuse area at the junction of tooth and bone with no apparent cement layer.

In horizontal section, many buccal dentary teeth show possible growth rings in the dentine (Pl. 67, fig. 2). These mark the boundary between primary dentine, laid down initially around the circumference of the tooth, and secondary dentine. Secondary dentine seems to be laid down in most teeth of *Hyperodapedon*, occluding the pulp cavity, but there is no regular pattern. Adjacent teeth may have root canals occluded to completely different extents, and the canal may become completely closed in the middle portion of the mandible (text-figs. 3*c–e*, 5). The root canal generally appears to remain open in all but the most anterior teeth (text-fig. 3*b*). The apical foramen is also usually open which indicates continued deposition of secondary dentine. The apical foramen may be axial, but it is frequently lateral, in which case the root tip is crescentic in section (text-fig. 6*a–c*; Pl. 66, fig. 2).

These lower parts of the teeth also show resorption effects. The tips of the roots are often randomly arranged (text-fig. 6*a–c*) and the growth of one clearly causes resorption of another along an arcuate front. This also occurs higher up where lingual teeth are growing close to buccal teeth, and one tooth achieves its normal form to the detriment of the other (text-fig. 3*d*; Pl. 67, fig. 5).

THE DENTITION OF *STENAULORHYNCHUS*

Arrangement of teeth in the maxilla

Stenaulorhynchus has two grooves on the maxillary tooth-plate. In juveniles, these lie between three distinct rows of teeth which are raised on sharp ridges (text-fig. 7*b*, *c*). However, in adults (text-fig. 7*e*, *g*), the grooves become apparently less regular as the teeth and bone are worn down. The medial groove runs the length of the maxilla, but the lateral one is restricted to the posterior portion. The grooves become shallower and rounded, and the teeth are not wholly restricted to the ridges. These facts suggest that the grooves in *Stenaulorhynchus* are initiated in the bone between the juvenile tooth rows, but that their subsequent appearance depends on wear to a far greater extent than in *Hyperodapedon* and other late Triassic rhynchosaurs, where the groove is a regular inherent part of the maxillary tooth-plate (Chatterjee 1974; Benton 1983*b*).

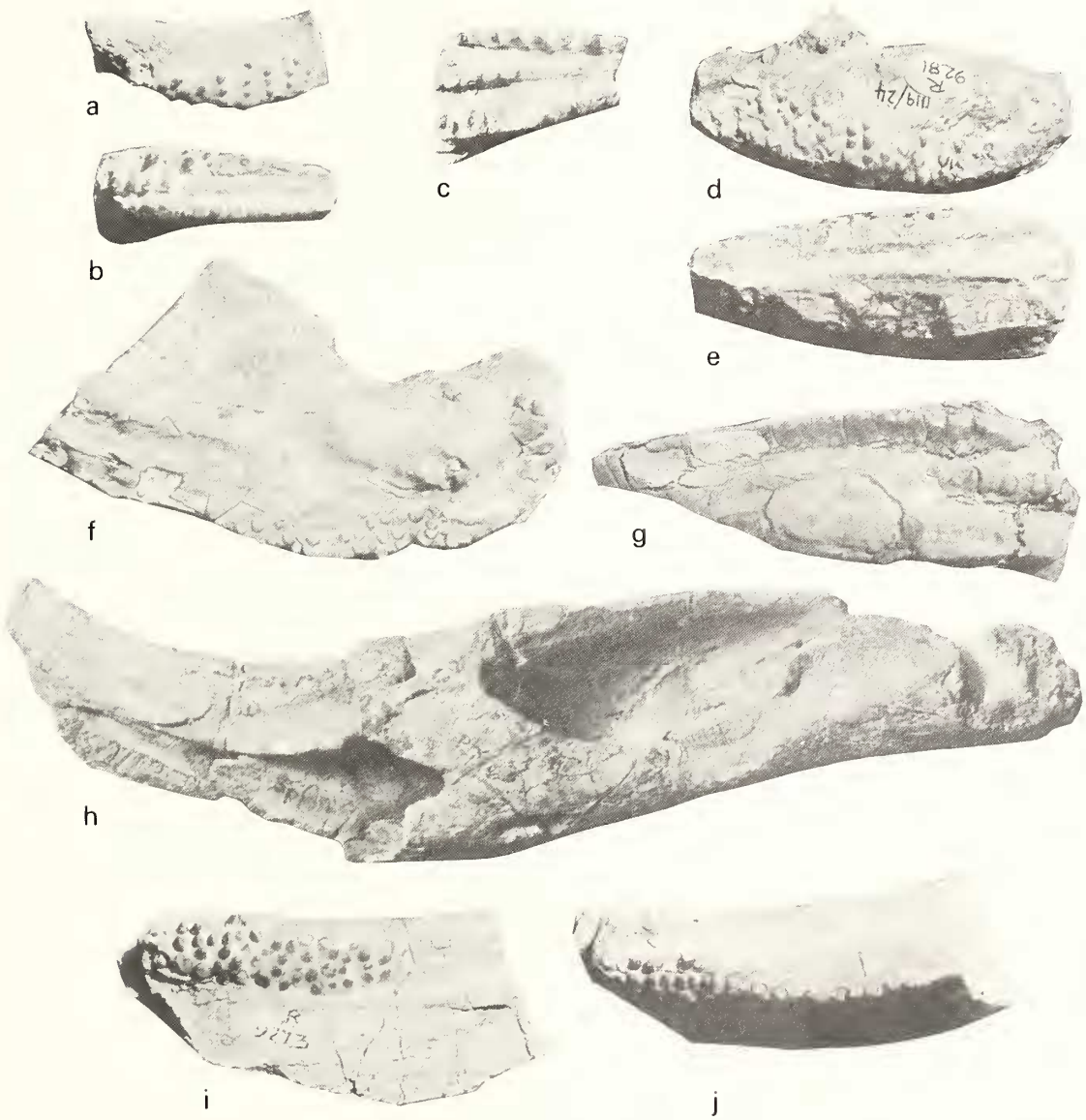
The teeth are arranged in longitudinal rows. In juvenile specimens (text-fig. 7*b*, *c*) there are three rows on the occlusal surface of the maxilla, the two outer ones running the length of the jaw, and the middle one only occupying the posterior third of the length. On the medial side of the maxilla (text-fig. 7*a*) a series of longitudinal rows of teeth may be seen running diagonally down and forwards to the crest of the jaw. Similar features may be seen in adult specimens (text-fig. 7*d–g*) where additional longitudinal rows are added to the occlusal surface from the medial diagonal rows. The pattern of tooth rows is generally regular, but a scattering of odd teeth that cannot easily be assigned to rows may occur in the medial groove (text-fig. 7*g*).

The tooth pattern of the maxilla of *Stenaulorhynchus* has been interpreted as consisting of distinguishable occlusal and lingual teeth (Huene 1938; Chatterjee 1974, 1980), but this is not an appropriate description. The 'lingual' diagonal rows all run to the jaw margin and continue without break on to the medial portion of the occlusal surface. It is not possible to distinguish between the 'occlusal' and the 'lingual' series of teeth in any specimen, and in terms of tooth growth the distinction is meaningless since 'lingual' teeth become 'occlusal' as the jaw is remodelled and worn (see below).

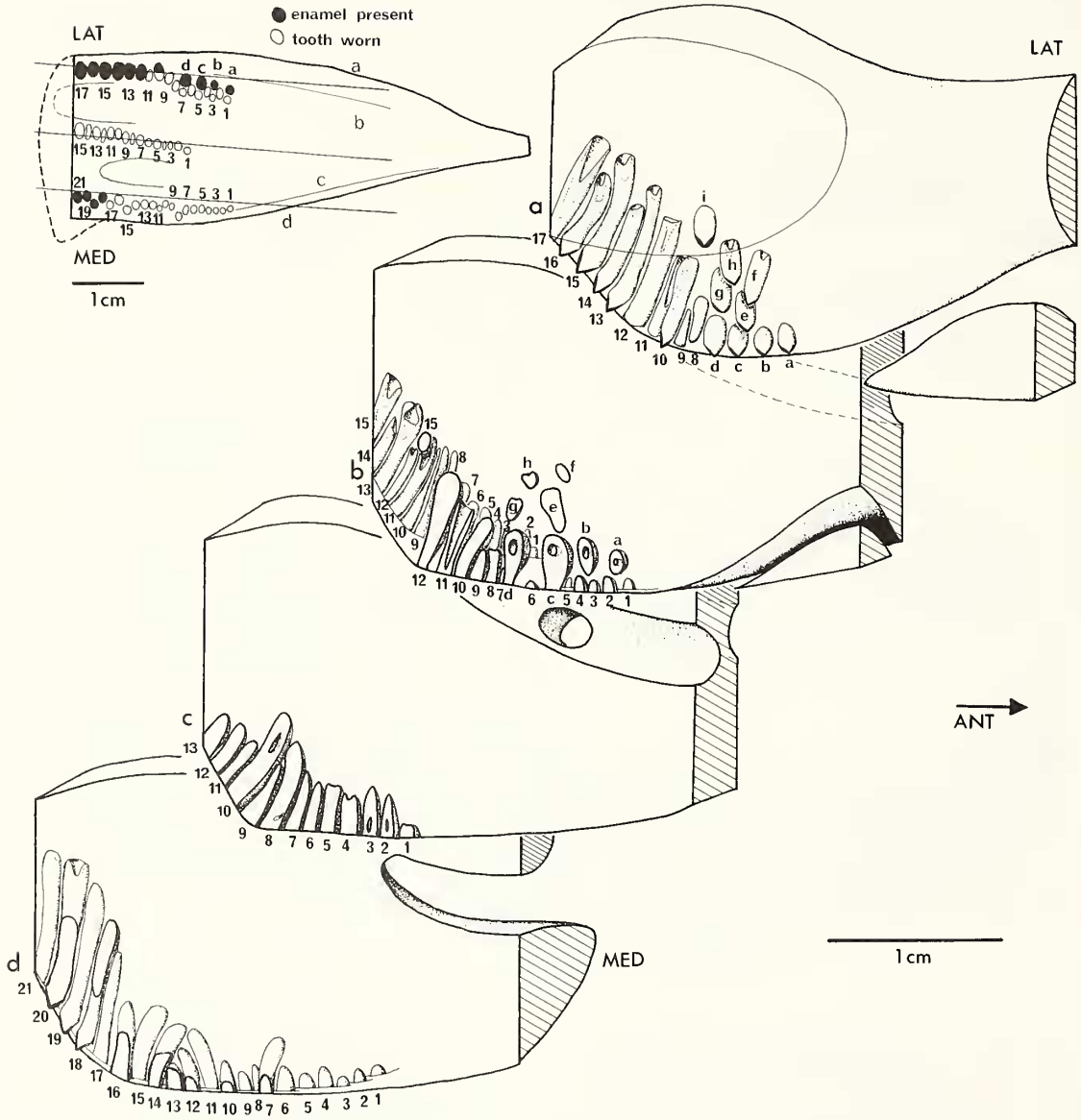
In order to check if any differences existed between longitudinal tooth rows, a series of longitudinal vertical sections through a complete maxillary tooth-plate was made. The three-dimensional reconstruction (text-fig. 8) shows the pattern of teeth in several longitudinal rows through the maxilla. Unfortunately, the most posterior portion of the tooth-plate was missing, and the youngest teeth cannot be shown.

The tooth arrangement is clearly rather irregular within individual longitudinal rows. Even the lateral row is not quite as simple as it appears in occlusal view (text-fig. 7*g*). In the example sectioned,

two series of teeth of rather different shape are involved, and they are cut at an angle by the plane of section (text-fig. 8). The anterior set consists of nine short teeth (*a–i*) with closed roots and enamel caps. None of these anterior teeth is particularly worn—they barely reach the occlusal margin in the side of the lateral groove—and the posterior one (*i*) does not erupt at all. The posterior set consists of seventeen long-rooted teeth (1–17), all of which have erupted. The anterior nine teeth (1–9)



TEXT-FIG. 7. Tooth-bearing bones of *Stenaulorhynchus stockleyi*: maxillae (*a–g*) and dentaries (*i, j*) (cf. text-fig. 14). *a, b*, juvenile left maxilla (BM(NH) R9279) in medial and occlusal views. *c*, juvenile left maxilla (CUMZ T993) in occlusal view. *d, e*, right maxilla (BM(NH)R9281) in medial and occlusal views. *f, g*, right maxilla (CUMZ T1138) in medial and occlusal views. *h*, right lower jaw (CUMZ T1112), lacking the splenial, in medial view (cf. text-fig. 9*c*). *i, j*, left dentary (BM(NH) R9273) in medial and occlusal views. All × 1, except *h*, × 0·71.



TEXT-FIG. 8. Graphic reconstruction of the dentition of the right maxilla of *Stenaulorhynchus* (BM(NH) R10008). Drawn from serial sections taken at 0·5 mm spacing, and traced on to glass plates at a magnification of 2 ×. The four block diagrams (*a–d*) are drawn as if the bone is transparent, and individual teeth are numbered or lettered in sequence from oldest to youngest in each row (see the text). The lines of section that separate the blocks are indicated on the occlusal view of the tooth-plate. The medialmost rows of teeth are missing owing to damage of the specimen. Abbreviations: ANT, anterior; LAT, lateral; MED, medial.

are heavily worn and rather mixed up with the anterior set just described. Of the posterior eight teeth, six (10, 13–17) still have their points and enamel caps, but the other two (11, 12) are worn. Two teeth (11, 17) have widely open roots—which indicates active deposition of dentine—and it could be that the posterior tooth series (1–17) splits into two longitudinal series (1–11, 12–17) where teeth 11 and 17 were initiated latest of all. In this case, it would be difficult to assign tooth 10 to either series.

The middle longitudinal series of fifteen teeth is easier to interpret. The teeth occur in one sequence, with the anterior group heavily worn, and the posterior group just coming into occlusion. The teeth in the latter group (11–15) have open roots. There is a considerable space between the middle row and the rows of the lingual (medial) side of the tooth-plate. The anterior teeth of the lingual rows are most heavily worn, and the posterior ones have open roots and unworn crowns. The twenty-one teeth are divided tentatively into three series (1–8, 9–15, 16–21), where the youngest teeth of each group are 6, 15, and 21. However, the sectioned maxilla does not show a well-developed battery of 'lingual' teeth, as in other jaws of similar size (e.g. text-fig. 7*f*, *g*), possibly as a result of damage, and this makes a full reconstruction difficult.

In summary, the teeth in the maxilla of *Stenaulorhynchus* are arranged in several longitudinal rows. There are three tooth-bearing areas in the tooth-plate: lateral, median, and medial. In the medial area, several diagonal rows of teeth pass into occlusion in sequence (text-fig. 8*b*), and there is no clear distinction between 'lingual' and 'occlusal' teeth.

Arrangement of teeth in the dentary

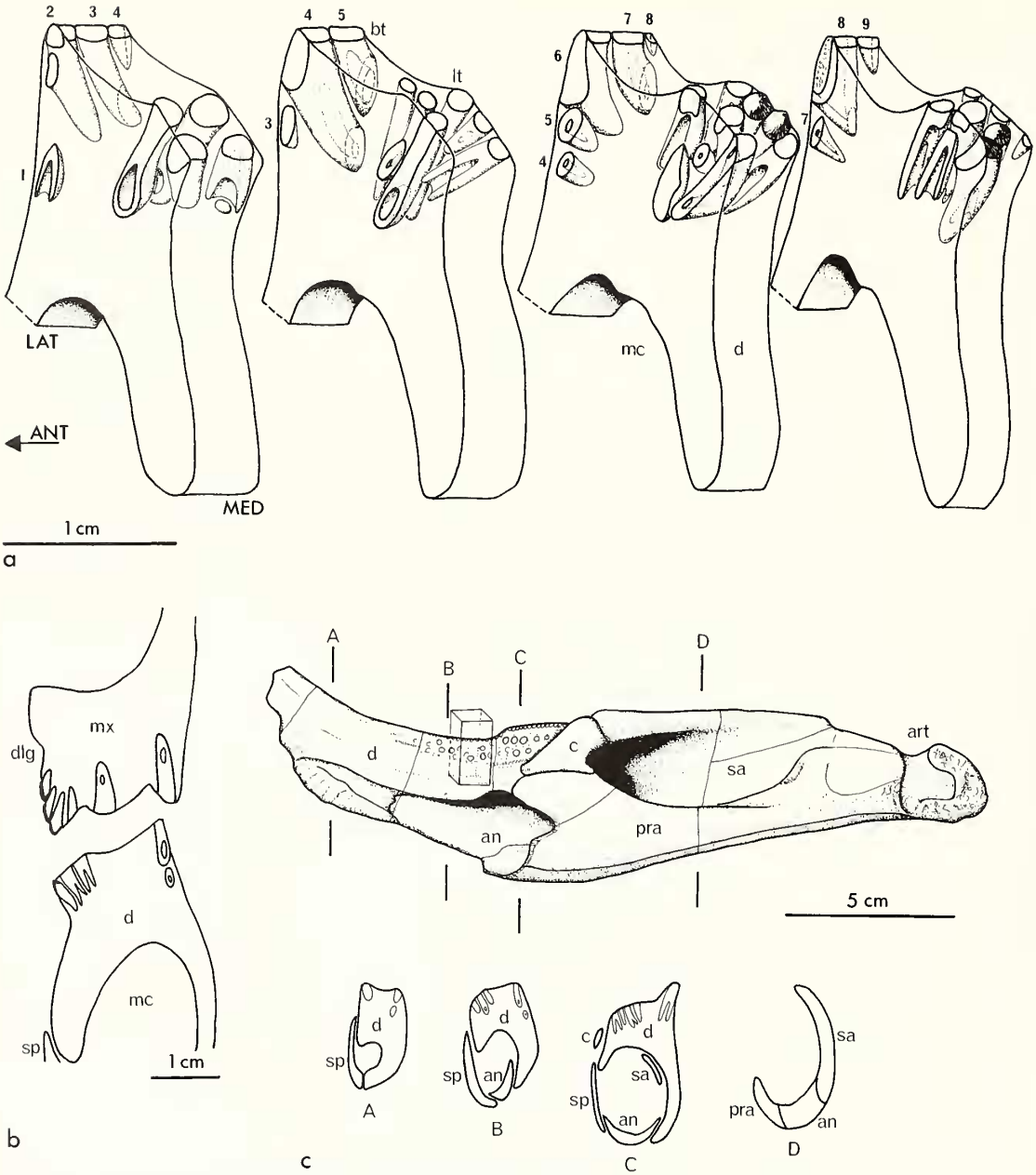
The lower jaw of *Stenaulorhynchus* (text-fig. 7*h*) is longer and lower than that of *Hyperodapedon* (c.f. text-fig. 1*c*, *d*) and the tooth-bearing portion is concentrated further forward. Well-preserved dentaries (text-fig. 7*i*, *j*) show that there is a raised longitudinal row of buccal teeth (lateral) and several diagonal rows of lingual teeth (medial) that run up into occlusion on top of the jaw. The lowest lingual teeth are small and occasional (?) replacement pits are seen (text-fig. 7*i*). The teeth are separated by a broad, shallow groove which changes in shape along its length. At the very back of the tooth row the posterior ten or twelve buccal teeth, which are not in occlusion, are raised on a high ridge and separated from the coronoid by a clear groove (text-fig. 9*c*).

A three-dimensional reconstruction of the *Stenaulorhynchus* dentary (text-fig. 9*a*) shows how the buccal teeth are deep-rooted and slope up and forwards, as in *Hyperodapedon*. The lingual teeth also slope up and forwards, but they also slope medially when low on the inside of the jaw. The most lateral tooth of the lingual series at any point is generally the largest and nearly all have open roots. The lingual teeth remain distinct from the buccal teeth, but there is little difference in shape or size between the two kinds, as seen in *Hyperodapedon*.

Jaw occlusion and tooth wear

Tooth and bone wear is clearly shown on the occlusal surfaces of the maxilla and dentary of *Stenaulorhynchus*. The relative curvature of the two tooth-bearing elements is not as great as in *Hyperodapedon*, and larger areas are in contact. Juvenile specimens show little wear (text-fig. 7*a–c*), but adult maxillae and dentaries (e.g. text-fig. 7*g*, *j*) are worn smooth except at the very back. The small enamel cap of each tooth is stained dark brown or black in some specimens, and this highlights the degree of wear (text-fig. 7*j*). As in *Hyperodapedon*, teeth generally bite against bone, although some medial teeth occlude (text-fig. 9*b*). Buccal teeth may be heavily worn on the lateral side of the dentary as well as on the occlusal surface (text-fig. 9*b*, *c*). Tooth and bone seem to wear at the same rate, and distinct pits or striations are not seen.

Stenaulorhynchus probably had a precision-shear bite, as in *Hyperodapedon*. The quadrate–articular joint appears to be rather tight (Huene 1938), and the strong symphysis would prevent rotation of the lower jaws—a necessary feature if they are to move back and forwards in such a broad skull. These points, and the apparent precise fit of dentary and maxilla, would prevent any marked fore and aft sawing of the jaws.



TEXT-FIG. 9. The right dentary of *Stenaulorhynchus* (BM(NH) R10007). *a*, graphic reconstruction of the dentition, drawn from serial sections taken at 0·5 mm spacing, and traced on to glass plates at a magnification of 2 ×. The single row of buccal teeth is numbered in sequence from the front backwards. The lingual teeth occur in several longitudinal rows, but these are rather confused by bone remodelling and relative tooth movement. *b*, transverse vertical section through the dentary and maxilla with the jaws slightly apart, to show the nature of the occlusion. A tooth may bite against another tooth, or against bone. *c*, medial view of a right lower jaw (CUMZ T1112, Songea district; cf. text-fig. 7*h*) which lacks the splenial (cf. *Hyperodapedon gordoni*, text-fig. 1*d*). The boxed region of the dentary is equivalent to that shown in the graphic reconstruction. Four cross-sections of the lower jaw at different positions along its length (A, B, C, D) are also given. Abbreviations: an, angular; ANT, anterior; art, articular; bt, buccal teeth; c, coronoid; d, dentary; dlg, dental lamina groove; LAT, lateral; lt, lingual teeth; mc, Meckel's canal; MED, medial; mx, maxilla; pra, prearticular; sa, surangular; sp, splenial.

Tooth form and histology

The teeth of *Stenaulorhynchus* are generally long-rooted and deeply fused in the bone of the jaw. The shapes are less regular than in *Hyperodapedon*, and the root canal is open in less teeth. The bulk of the tooth is composed of dentine, and unerupted or unworn teeth may display a small cap of enamel.

Tooth shape and size vary slightly across the maxilla. In juveniles, most teeth are unworn and their round conical pointed shape may be seen (text-fig. 7*a–c*). It is not possible to distinguish 'lingual' from 'buccal' teeth as in *Hyperodapedon*. In older specimens, most of the occlusal teeth are worn flush with the surrounding bone (text-figs. 7*d–g*, 10*a*, *b*). Teeth of the lateral row are nearly always larger than the others (2–3 mm in diameter, compared with 1–2 mm or less). They are rather compressed, or oval, in shape, with the long axis directed transversely—this may be a result of their tight packing with only a thin wall of intervening bone. Other maxillary teeth are more circular in cross-section. The teeth on the lingual surface are small and unworn. They are pointed and conical and still retain their enamel caps (text-figs. 7*a*, *d*, *f*, 11*b*).

Teeth are generally absent from the most anterior portion of the maxilla—they have presumably been completely worn away. Tooth size increases backwards from the short heavily worn teeth at the front to the middle of the area currently in occlusion, where the teeth have the longest roots (text-figs. 7*g*, 10). They then diminish to the back of the jaw, where the most posterior, youngest, teeth have not yet come into occlusion.

Some anterior teeth in the lateral series are short and rounded (text-figs. 10*a*, 12*c*). Other teeth are long and compressed, or resorbed in an irregular way under the influence of neighbouring teeth. A selection of tooth shapes may be seen in text-figs. 10 and 12*a–d*. Newly formed teeth have open apical foramina and wide root canals surrounded by a thin tube of dentine (text-fig. 12*a*), while older teeth show signs of irregular resorption and irregular closure of the root canal (text-fig. 12*b*). The root canal becomes occluded (text-fig. 12*c*), and finally, heavily worn teeth may be resorbed at the base by the surrounding bone (text-fig. 12*d*). The teeth are circular to oval (long axis transverse to axis of jaw) in cross-section.

A transverse section of a *Stenaulorhynchus* maxilla (text-fig. 11*b*) shows how successive longitudinal rows of 'lingual' teeth grow down into the teeth below. Each tooth bears an enamel cap that extends further medially where it erupts on the inside of the jaw, and the teeth in occlusion are worn flush with the surface of the bone.

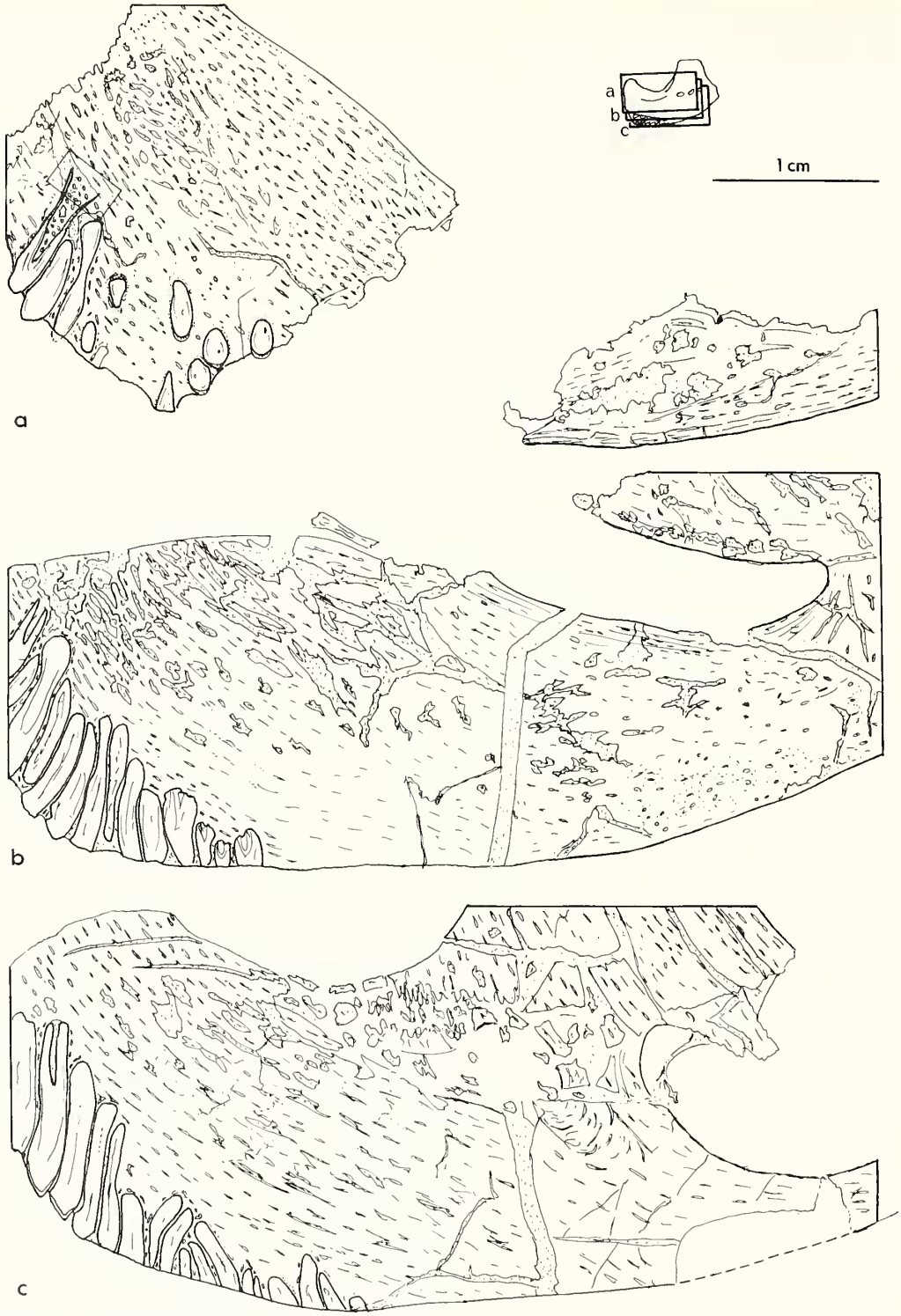
Teeth are present in middle and posterior portions of the occlusal edge of the dentary. Teeth are absent from the very front of the jaw (text-fig. 11*c*), but they may be seen in the buccal row a short distance back (text-fig. 11*d*). Here, the lower portion of the next tooth has an open root canal. Further back, the buccal teeth are deeply rooted, and they slope up and forwards (text-fig. 11*e*, *f*). The lingual teeth slope up, forwards, and medially. They often have open root canals, and the enamel caps may be seen when the teeth are not in occlusion (text-fig. 11*f*). The teeth are cylindrical, but the shape may be disturbed by irregular resorption as a result of close-packed neighbouring teeth. Tooth shape is just as variable in the maxilla. Newly formed teeth have large root canals (text-fig. 12*e*), which become partly closed off (text-fig. 12*b*) and occluded, often in an irregular way (text-fig. 12*g*). The relationships between neighbouring lingual teeth may be complex (text-fig. 12*h*). Resorption of teeth at the base is not seen in the dentary as much as in the maxilla.

Bone and tooth histology

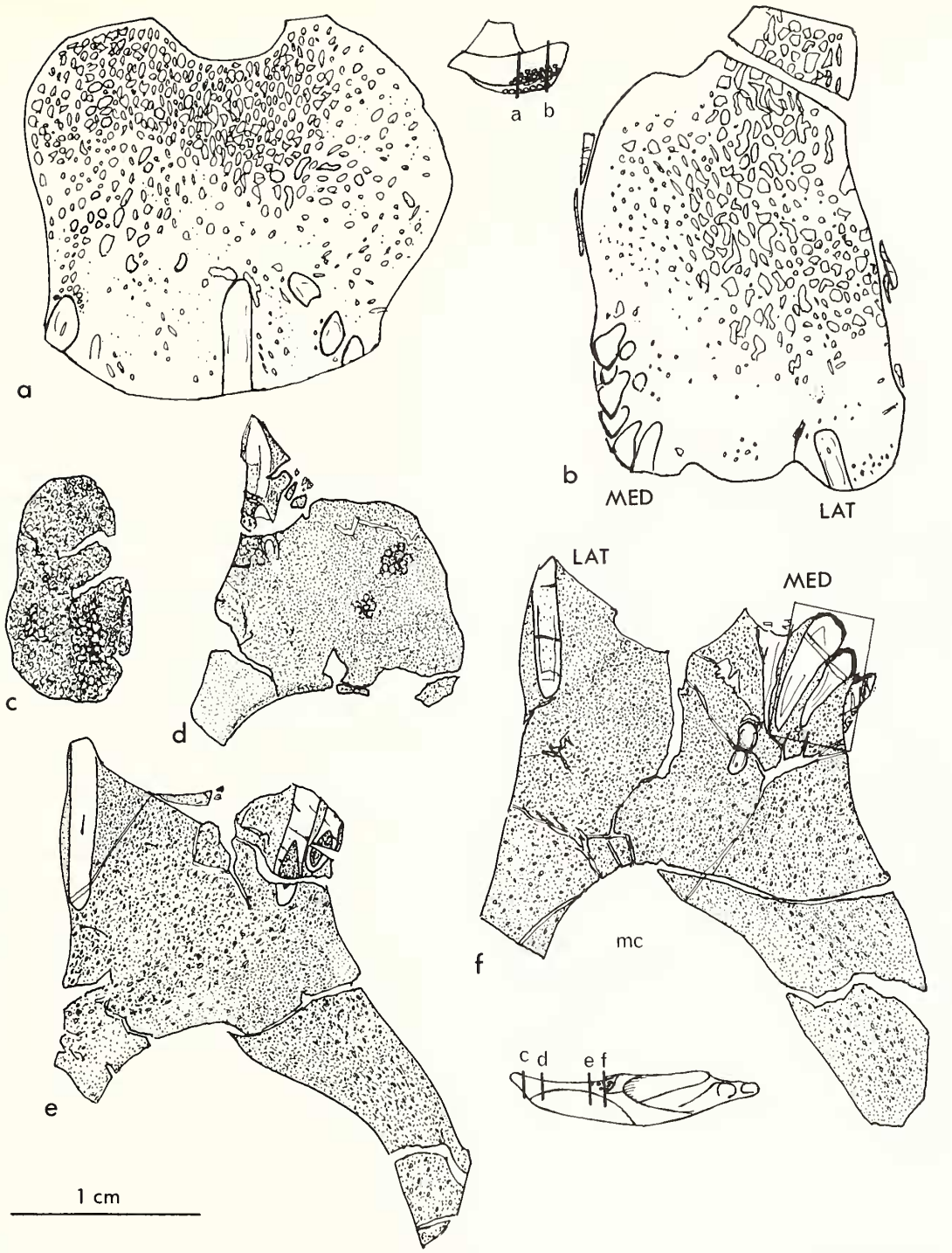
As with *Hyperodapedon*, the serial peels and microscopic sections of *Stenaulorhynchus* jaws have shown a great deal of histological detail. The bone of the jaws includes four types:

1. Avascular lamellar-zonal periosteal bone in the anterior occlusal edge of the maxilla (text-fig. 10*a*) and around blood vessel canals (Pl. 68, fig. 1) where the 'track' of the vessel as the bone grows may be seen.

2. Laminar fibrolamellar bone with parallel longitudinal primary osteons in regions with teeth (text-figs. 10, 11; Pl. 68, fig. 5).



TEXT-FIG. 10. Longitudinal vertical sections of the maxilla of *Stenaulorhynchus* (BM(NH) R10008) showing teeth. The locations of the sections are indicated on an outline maxilla. *a*, lateral tooth row; several largely unworn teeth are shown, one with a wide open root canal. This shows teeth numbered as *a*–*d*, 10, 13–17 (text-fig. 8). The boxed area is shown at higher magnification in Pl. 68, fig. 2. *b*, middle tooth row; the youngest (left-hand) tooth has an open root, while the oldest (right-hand) teeth show resorption of the base. This shows teeth numbered as 2–15 (text-fig. 7). *c*, medial tooth row(s); anterior teeth are heavily worn and resorbed. This shows teeth numbered as 5–21 (text-fig. 9).



TEXT-FIG. 11. Transverse vertical sections of the right maxilla (*a*, *b*) and right dentary (*c–f*) of *Stenaulorhynchus*. The locations of the sections are indicated on an outline maxilla and lower jaw. *a*, *b*, cross-sections of the maxilla, traced from polished end sections (BM(NH) R9276, R9277), and showing the arrangement of teeth in the lateral, middle, and medial rows. Lingual teeth of young (high) Zahnreihen can be seen to have caused erosion of older teeth in *b*. The dentary: *c*, anterior portion where the bone is compact and the teeth have been worn away and resorbed; *d*, further back, worn buccal teeth may be seen on the lateral side; *e*, in the occlusal area, large buccal and lingual teeth are present, with open root canals; *f*, at the back, some teeth are in occlusion, and others with unworn enamel caps have just been implanted. The boxed area is shown at higher magnification in Pl. 68, fig. 6. Abbreviations: LAT, lateral; mc, Meckel's canal; MED, medial.

3. Reticular (cancellous) fibrolamellar bone in the centre of bones and away from the teeth (text-figs. 10, 11).

4. Bone of attachment: secondary reticular fibrolamellar bone surrounding teeth and cross-cutting laminar fibrolamellar bone. The sheath of reticular bone surrounds each tooth and accompanies it through the jaw (text-figs. 10, 11; Pl. 68, figs. 3, 4, 6). Between close-packed teeth, the osteons of the bone of attachment may be distorted and flattened (Pl. 68, figs. 4, 6). The bone is especially cancellous at the base of teeth, and spongy reticular bone may fill the wide open root canals of newly formed teeth (Pl. 68, fig. 2).

Micrographs of the bone of *Stenaulorhynchus* maxillae and dentaries show osteocyte lacunae, and the centripetal arrangement of finely lamellated bone in primary osteons around vascular canals is clear (e.g. Pl. 68, figs. 5, 7).

Enamel is present in a cap on most unerupted or unworn maxillary and dentary teeth (Pl. 68, figs. 3, 6), but the crystal structure is not seen. The enamel cap is very small and covers only the tip of the tooth and the exposed sides of those that erupt first on the lingual side of the maxilla or dentary. The enamel is soon worn away when teeth come into occlusion (text-fig. 7*j*). The dentine clearly shows radial dentinal tubules (Pl. 68, figs. 7, 8), as in *Hyperodapedon*.

Growth lines (contour lines of Owen) in the dentine are very clear (text-fig. 12; Pl. 68, figs. 3, 4, 6–8) and these are marked by bends in the dentinal tubules. They clearly show the sequential centripetal filling of the pulp cavity, with periods of slow and fast deposition of secondary dentine. Adjacent teeth show matching sequences of dark and light, and broad and narrow bands (Pl. 68, fig. 4), and these catalogue periods of growth (food availability/seasonality?).

The effects of resorption of tooth material may be seen in several ways. Adjacent teeth may cause extensive resorption along an arcuate front where they contact their neighbours and give rise to irregular constrictions and bends (e.g. text-figs. 10, 11), and, in some cases, teeth are excluded from the jaw margin by others (text-fig. 10*b*). The resorption cuts through the incremental lines in the

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EXPLANATION OF PLATE 68

The dentition and bone of the maxilla (figs. 1–4) and dentary (figs. 5–8) of *Stenaulorhynchus*. Sections from BM(NH) R10008 (figs. 1–4) and BM(NH) R10007 (figs. 5–8).

Fig. 1. Longitudinal vertical section through the anterior portion of the maxilla, showing the laminar fibrolamellar bone with the canals running up and backwards, and two small blood-vessels and their 'tracks' of remodelled bone also running up and backwards, × 4·5.

Fig. 2. Longitudinal vertical section through the root apex of a posterior tooth, showing the widely open root canal filled with spongy bone and the bone of attachment, set in the normal laminar fibrolamellar bone of the jaw; this section is located in text-fig. 13*a*, × 17.

Fig. 3. Longitudinal vertical section through some unerupted anterior teeth of the lateral series, showing the bone of attachment, the circumferential growth lines in the dentine and erosion of an older (lower) tooth in the bottom right-hand corner, by a younger (higher) tooth, × 12.

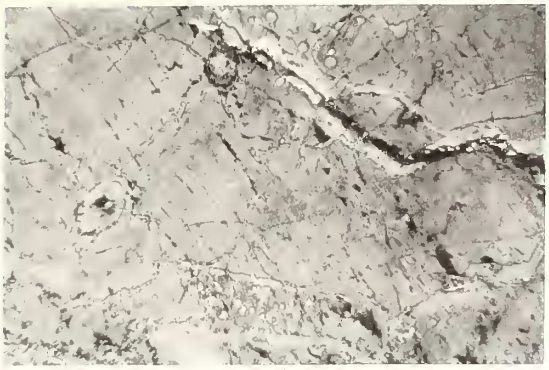
Fig. 4. Longitudinal vertical section through some anterior heavily worn teeth (occlusal margin at foot of picture), showing dentine growth lines, fully closed root canals, irregular resorption of the base of the teeth, and associated irregular bone, × 12.

Fig. 5. Transverse vertical section, showing typical primary osteons of the laminar fibrolamellar bone, × 30.

Fig. 6. Transverse vertical section through two lingual teeth, showing the unworn enamel caps, growth rings in the dentine, and erosion of the side of the older (left-hand) tooth by the younger (right-hand) tooth; this section is localized in text-fig. 11*f*, × 12.

Fig. 7. Transverse vertical section through part of a lingual tooth showing the bone of attachment, the root canal, secondary dentine with growth rings, and radial dentinal tubules, × 25.

Fig. 8. A similar transverse vertical section through parts of two lingual teeth with occluded root canals, showing the relationship between the growth lines in the secondary dentine and the radial dentinal tubules, × 45.



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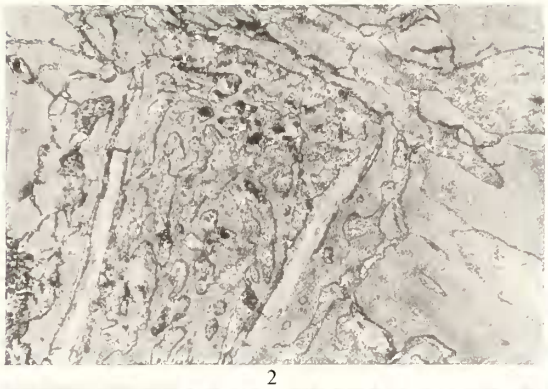

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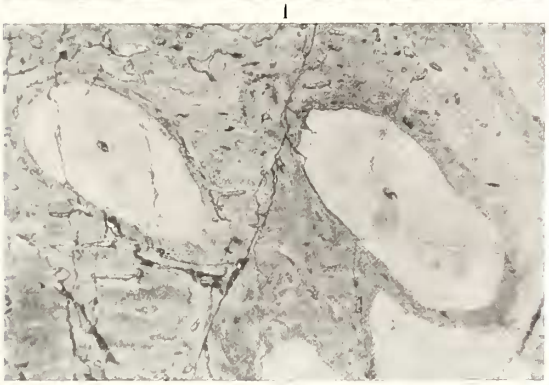

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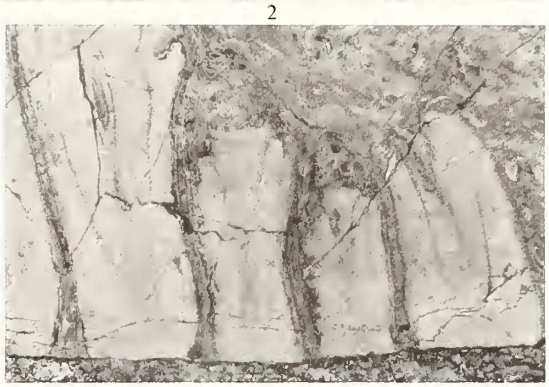

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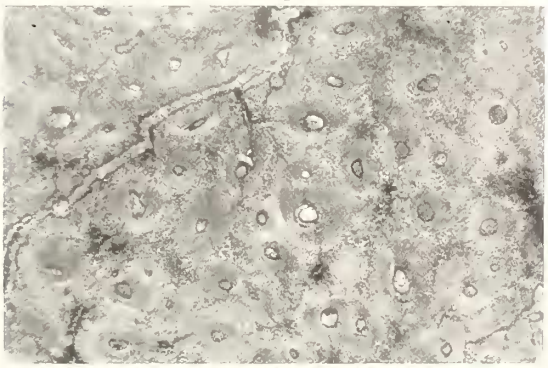

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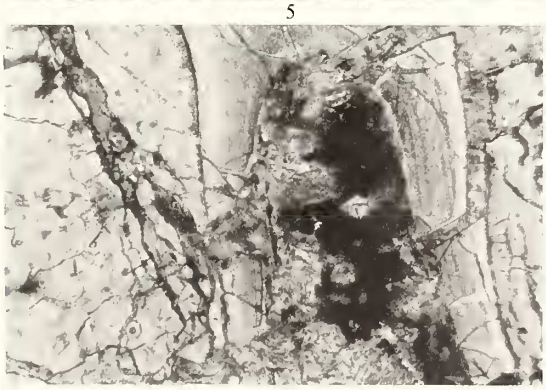

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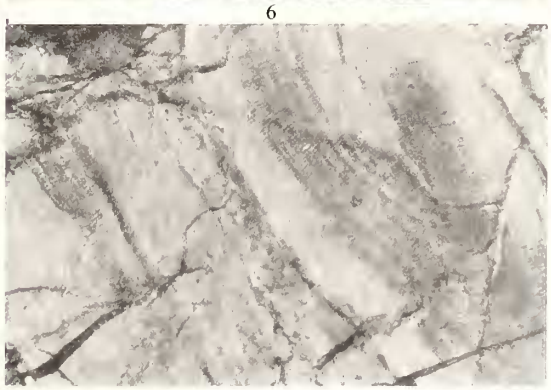
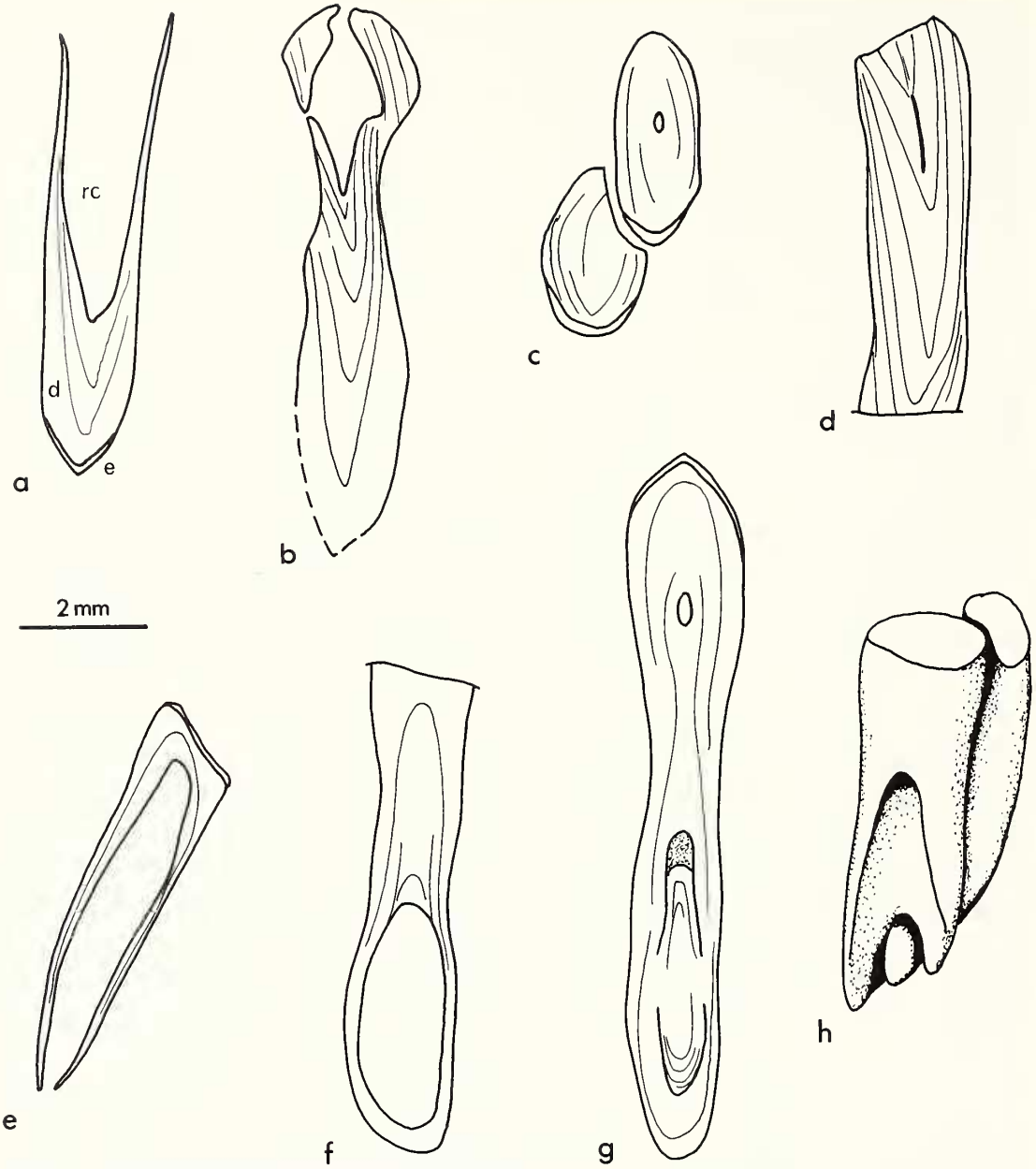


8

BENTON, rhynchosaur dentitions



TEXT-FIG. 12. Sketches of individual teeth of *Stenaulorhynchus*: *a–d*, from the maxilla with the crown facing downwards; *e–h*, from the dentary, with the crown facing upwards. *a*, newly implanted tooth with open root canal, some secondary dentine deposition and an unworn enamel cap; *b*, slightly older tooth, partly worn, with more deposition of secondary dentine, and irregular closure of the root canal owing to extensive erosion by neighbouring teeth; *c*, two small unerupted teeth with complete enamel caps, and 'interference' in which the younger (upper) one causes erosion of the older (lower) one; *d*, an old heavily worn tooth in which the root canal has been completely occluded, and resorption of the base has begun; *e*, a newly implanted lingual dentary tooth in which little secondary dentine has been deposited; *f*, an older lingual tooth in which the crown is worn, but the root canal is still open; *g*, a large lingual tooth with unworn enamel cap and extensive occlusion of the root canal by secondary dentine; *h*, graphic reconstruction of two lingual teeth which have been implanted so close together that each has interfered with the normal development of the other. Abbreviations: d, dentine; e, enamel; rc, root canal.

dentine, and may open up the root canal (text-fig. 12*b*). In other cases, the crown of a growing tooth may pass through the root of a tooth in occlusion and cause loss of dentine in the latter (text-fig. 12*c*; Pl. 68, fig. 3). This pattern of extensive resorption is more common in *Stenaulorhynchus* than in *Hyperodapedon*, as is resorption of the base of old worn teeth by the surrounding bone (text-figs. 10*b*, 12*d*). This resorption occurs especially in the maxilla where the bone of attachment can be seen to invade the dentine, often along particular growth lines, leaving the root of the tooth ragged and incomplete (Pl. 68, fig. 4).

TOOTH IMPLANTATION IN RHYNCHOSAURS

Rhynchosaurs have deeply rooted teeth fused to bone of attachment. They show a combination of features of both the thecodont and acrodont systems, and Chatterjee (1974) has termed this mode of attachment 'ankylothecodont'. A characteristic feature is the secondary bone of attachment which has also been identified in *Scaphonyx fischeri* (Sill 1971*b*, pl. 4c) and *H. huxleyi* (Chatterjee 1974, p. 230). The latter author described this bone of attachment as 'spongy in appearance resembling a foam of very small bubbles', and it is clearly demarcated from the surrounding bone. *H. gordoni* does not show the 'bony layered structure . . . at the base of some teeth, invading the pulp cavity' observed by Chatterjee (1974) in *H. huxleyi*, but reticulate bone has been noted above in the pulp chamber of *Stenaulorhynchus*.

Most early reptiles (e.g. pelycosaurs, captorhinomorphs, early diapsids) had subthecodont (= protothecodont) tooth implantation (Edmund 1969). In *Captorhinus* the subthecodont teeth have relatively shallow roots and they are ankylosed into a socket by bone of attachment with 'no space . . . for a periodontal ligament or other soft tissues between the socket and the base of the tooth' (Bolt and DeMar 1975). Most early diapsids have also been stated to have subthecodont teeth, and that is probably the primitive character for the group (Benton 1983*b*), although there is much confusion about the terminology here, and detailed histological information is needed. Some diapsids evolved thecodont teeth in the Triassic (thecodontians, dinosaurs, crocodiles), while others evolved acrodont teeth (sphenodontids) or 'subpleurodont' teeth (early squamates). The rhynchosaurs evolved a fourth system—ankylothecodont teeth (deeply rooted teeth surrounded by bone of attachment which may also invade the pulp chamber; no 'socket' with soft tissues around the teeth; no typical reptilian tooth replacement).

The acrodont agamid lizard *Uromastix* may also show a bony core in the pulp chamber of posterior teeth, but its function is uncertain (Throckmorton 1979). An analogous condition also occurs in adult *Sphenodon*. Secondary bone grows round the bases of the teeth and encloses many of them in shallow alveoli. The teeth are still firmly fused with the base and sides of the alveoli and are thus not thecodont. Howes and Swinnerton (1901) and Harrison (1901) describe this condition in *Sphenodon* as 'hyperacrodont'.

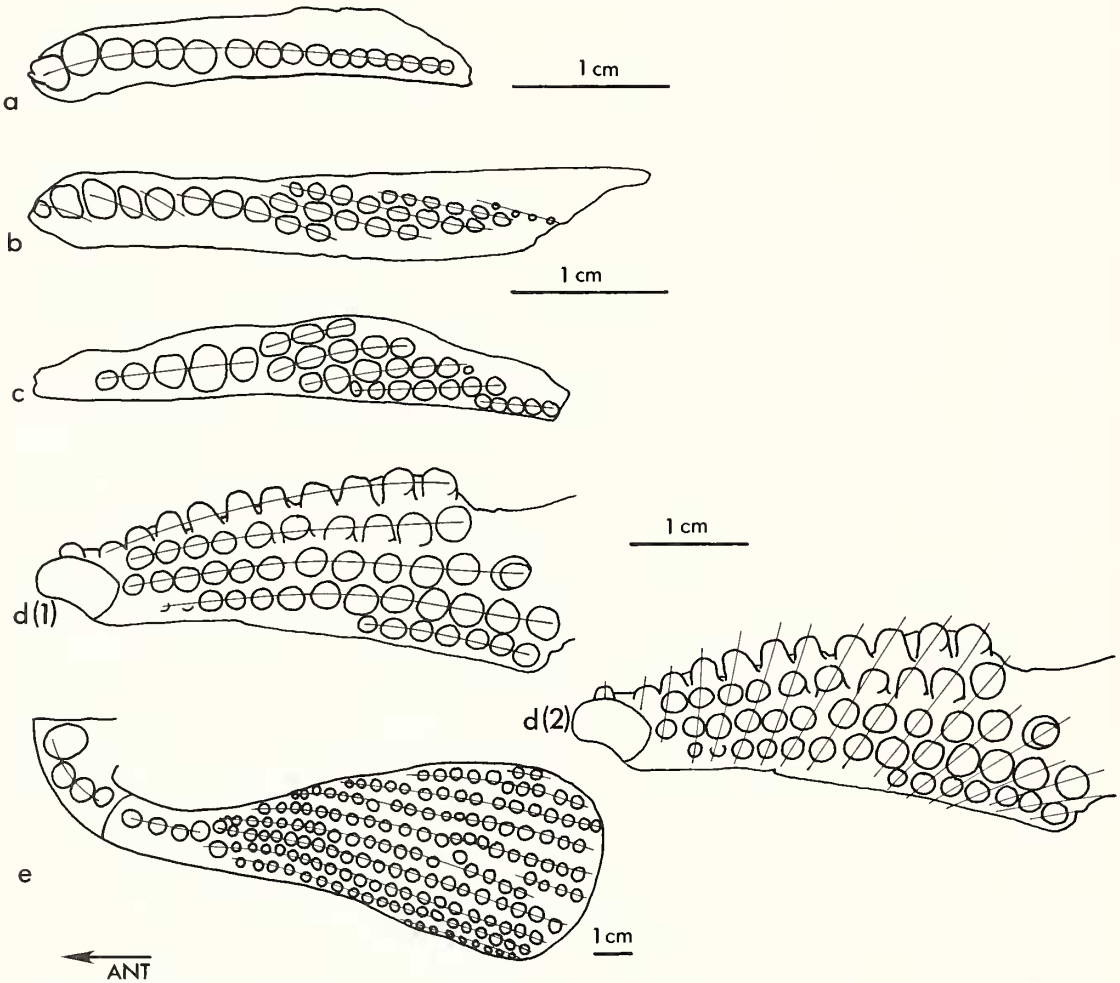
TOOTH ADDITION IN RHYNCHOSAURS

The multiple row dentition of the rhynchosaur maxilla and dentary has been interpreted as the retention in the adult of an embryonic type of dentition, with the diagonal tooth rows equivalent to the Zahnreihen of Woerdemann (1921) (Edmund 1960, p. 59; 1969, p. 153; Chatterjee 1974, p. 234). The captorhinomorphs *Captorhinus*, *Labidosaurikos*, and *Moradisaurus* also retain apparently similar diagonal rows of functional teeth in the adult, and a brief consideration of these early reptiles may throw light on the development of the rhynchosaur dentition.

Multiple tooth rows in captorhinomorphs

Early captorhinomorphs, such as *Eocaptorhinus laticeps* from the lower Permian of Texas and Oklahoma, had a single-row dentition of subthecodont teeth in premaxilla–maxilla and dentary (text-fig. 13*a*). There is evidence of tooth replacement from below (replacement gaps, replacement scars), and the tooth rows have been divided tentatively into Zahnreihen (Heaton 1979).

The slightly later *C. aguti* (lower Permian, Texas, New Mexico, Oklahoma) normally has three or four clear subparallel postero-medially directed rows (total range, one to eight rows) of subthecodont teeth on premaxilla–maxilla and dentary (text-fig. 13*b*, *c*). Bolt and DeMar (1975) and Ricqlès and Bolt (1983) have demonstrated that all teeth were continuously replaced and that the number of teeth and of rows did not depend on the size of the animal. Each diagonal row is interpreted as a Zahnreihe, and tooth replacement proceeded in such a way that matching diagonal rows of lower and upper teeth were maintained for an efficient shearing jaw action. Teeth were replaced from a lingually situated dental lamina at the posterior end of each Zahnreihe, and teeth were lost anteriorly/labially. There was a limit to this addition, and at times whole Zahnreihen would be lost anteriorly.



TEXT-FIG. 13. Occlusal views of the jaws of captorhinomorphs, showing the teeth in outline: *a*, right dentary of *Eocaptorhinus*; *b*, right dentary of *Captorhinus*; *c*, right maxilla of *Captorhinus*; *d*, right maxilla of *Labidosaurikos*; *e*, right maxilla of *Moradisaurus*. Zahnreihen are indicated with thin lines; two alternative interpretations are given for *Labidosaurikos*, in terms of Zahnreihen (*d* (1)) and tooth families (*d* (2)). (*a*, after Heaton 1979; *b*, *c*, after Ricqlès and Bolt 1983; *d* (1), after Edmund 1960; *d* (2) after Osborn 1977; *e*, after Ricqlès and Taquet 1982).

Several captorhinomorphs had yet more highly developed mutliple tooth rows: *Labidosaurikos* from the lower Permian of Oklahoma and Texas had four or five long diagonal rows of teeth in each jaw (text-fig. 13*d*). Edmund (1960, pp. 31–32) compared tooth replacement in the maxilla of *L. bakeri* with *C. aguti*. His view was that *C. aguti* did not have tooth replacement and that Zahnreihen were added lingually throughout life. Edmund assumed that the posterior rows of small teeth were present in the juvenile and that teeth were added only anteriorly and lingually. He did not make it clear how this model applies to *Labidosaurikos*, but the available figures and descriptions (Stovall 1950; Olson 1954; Seltin 1959; Edmund 1960, p. 31) clearly do not support his view of anterior tooth addition. Heaton (1979, p. 22) noted that a simple model of replacement waves of teeth erupting lingually and displacing existing tooth generations labially could give rise to the pattern seen in *Labidosaurikos*. However, the specimens must be restudied in order to determine whether replacement from below occurred, whether teeth were added to the postero-lingual ends of Zahnreihen, and whether the Zahnreihen migrated labially.

The upper Permian captorhinomorph *Moradisaurus* from the Niger (Taquet 1969; Ricqlès 1980; Ricqlès and Taquet 1982) had eleven to twelve longitudinal rows of teeth in the maxilla (text-fig. 13*e*). *Moradisaurus* had a very large skull (*c.* 40 cm long) which was broad posteriorly, as in rhynchosaurs. However, it did not have the groove in the maxillary tooth-plates typical of most rhynchosaurs.

Osborn (1977) has recently reinterpreted the multiple-row captorhinomorph dentition in terms of tooth families and inhibitory control of tooth alternation (cf. text-figs. 13*d* (1) and 13*d* (2)). The Zahnreihe and inhibitory models, as applied to more typical polyphyodont reptiles, must be compared as explanations of multiple tooth rows in captorhinomorphs and rhynchosaurs.

Development of patterns in reptile dentitions

In most reptiles, teeth are replaced continuously throughout life. New teeth are initiated deep within the jaw and as they grow they pass towards the jaw margin where they erupt and function for a few months before being replaced from below. The teeth are replaced in regular waves which sweep through alternate tooth positions generally from the back to the front of the jaw. Diagonal rows of developing teeth are termed Zahnreihen and vertical lines of teeth initiated at specific positions are called tooth families. The problem is to determine whether either of these pattern lines has a biological significance.

Edmund (1960) suggested that Zahnreihen are the key to reptile tooth replacement. A stimulus passes from the front to the back of the jaw and initiates the development of a new tooth at each tooth position. New stimuli are regularly initiated and several Zahnreihen are being developed at any time.

Osborn (1970, 1972) argued that Zahnreihen have no biological meaning. He proposed (Osborn 1971, 1974, 1977) that teeth may be initiated anywhere along the dental lamina, and that the spacing and rate of growth are controlled by the production of a fixed area of inhibition around a tooth germ, which reduces as the tooth grows. According to this model, descriptive units such as Zahnreihen, tooth families, and replacement waves have no developmental significance since they are subjectively selected by the observer (Osborn 1977). They are the result of the ontogeny of the teeth.

A problem arises here in that the 'Zahnreihen theory' of Edmund (1960) and the 'inhibition theory' of Osborn (1971, 1977) are not opposites that can be tested against each other. The former has not been fully developed as a theory of causation (DeMar and Bolt 1981) and experiments have not been designed to test the inhibition theory (Osborn 1974, 1977). Osborn (1971) found that tooth families were better units to use than Zahnreihen in interpreting the dentition of the lizard *Lacerta vivipara*. He later (Osborn 1977) interpreted the dentition of *Captorhinus* and *Labidosaurikos* in terms of the inhibition model and tooth families (text-fig. 13*d* (2)). On the other hand, Bolt and DeMar (1975) and Ricqlès and Bolt (1983) concluded that Zahnreihen provided the simplest explanation of the dentition of *Captorhinus*, and an examination of the multiple tooth rows of other captorhinomorphs confirms this descriptive interpretation of the pattern. The longitudinal diagonal rows are far more obvious as independent units than any other lines selected. The Zahnreihen terminology will also be used here for rhynchosaurs on the grounds of simplicity of description.

Interpretation of the rhynchosaur dentition

The functioning dentition of rhynchosaurs consists of several longitudinal or longitudinal/diagonal Zahnreihen. Teeth were not replaced from below but their root canals remained open while they were in occlusion. Teeth were formed on a dental lamina which lay lingual and posterior (*Stenaulorhynchus*) or posterior (*Hyperodapedon*) to the tooth-bearing bones. Teeth became ankylosed to the jaw adjacent to the dental lamina and out of the zone of occlusion. With growth of the upper and lower jaws, the area of wear expanded backwards and lingually. New teeth came into occlusion at the back and lingual side of the jaw and worn teeth at the front ceased to be used and became partly resorbed. Thus, teeth were added simultaneously to the posterior ends of several Zahnreihen which were losing teeth anteriorly, by remodelling and growth of the jaw. There was no extensive 'drift' or migration of teeth through the bone of the jaw, as has also been shown in *Captorhinus* (Ricqlès and Bolt 1983). In addition, Zahnreihen were initiated posteriorly and lingually as the dentigerous bones increased in size.

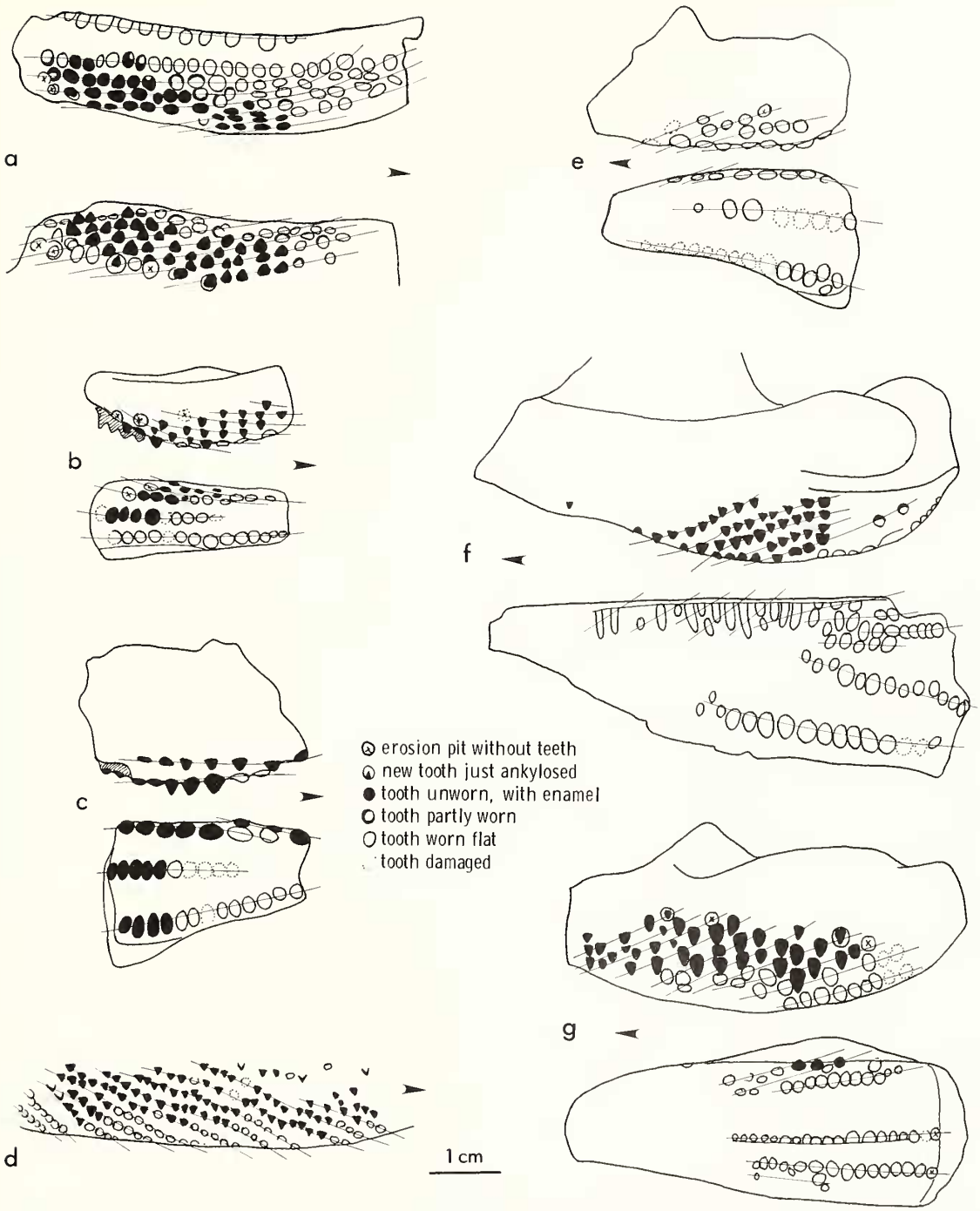
The assignment of teeth to Zahnreihen is relatively easy in *Stenaulorhynchus* (text-fig. 14). The rows may overlap slightly, but teeth are not exchanged between Zahnreihen. However, in *Hyperodapedon* (text-fig. 15) and other late Triassic rhynchosaurs the assignment is more difficult. Chatterjee (1974, pp. 230, 234) showed two ways of distinguishing tooth rows in maxillae of *H. huxleyi*: longitudinal rows and transverse rows. Longitudinal rows were easier to establish in young specimens, whereas transverse rows were more obvious near the posterior margin in large specimens. Chatterjee interpreted the transverse rows as Zahnreihen, and envisaged the regular addition of new rows posteriorly as soon as the jaw grew sufficiently. However, this is a misinterpretation of the meaning of Zahnreihen (Edmund 1960; DeMar 1974; Bolt and DeMar 1975), which may be regarded simply as rows of teeth in which relative age increases progressively from back to front. The last ankylosed tooth and the dental lamina are in the posteriormost position. Edmund (1960, p. 59) and Malan (1963) have also interpreted the longitudinal tooth rows in *Howesia*, a primitive rhynchosaur from the early Triassic of South Africa, as Zahnreihen.

The pattern of teeth that is seen on the occlusal surface of the rhynchosaur jaw is clearly much modified by jaw growth and remodelling and by 'interference' between individual teeth. The more anterior the position of a tooth, the older it is, and the more it will have been affected by events subsequent to budding and ankylosis.

Posterior addition of teeth

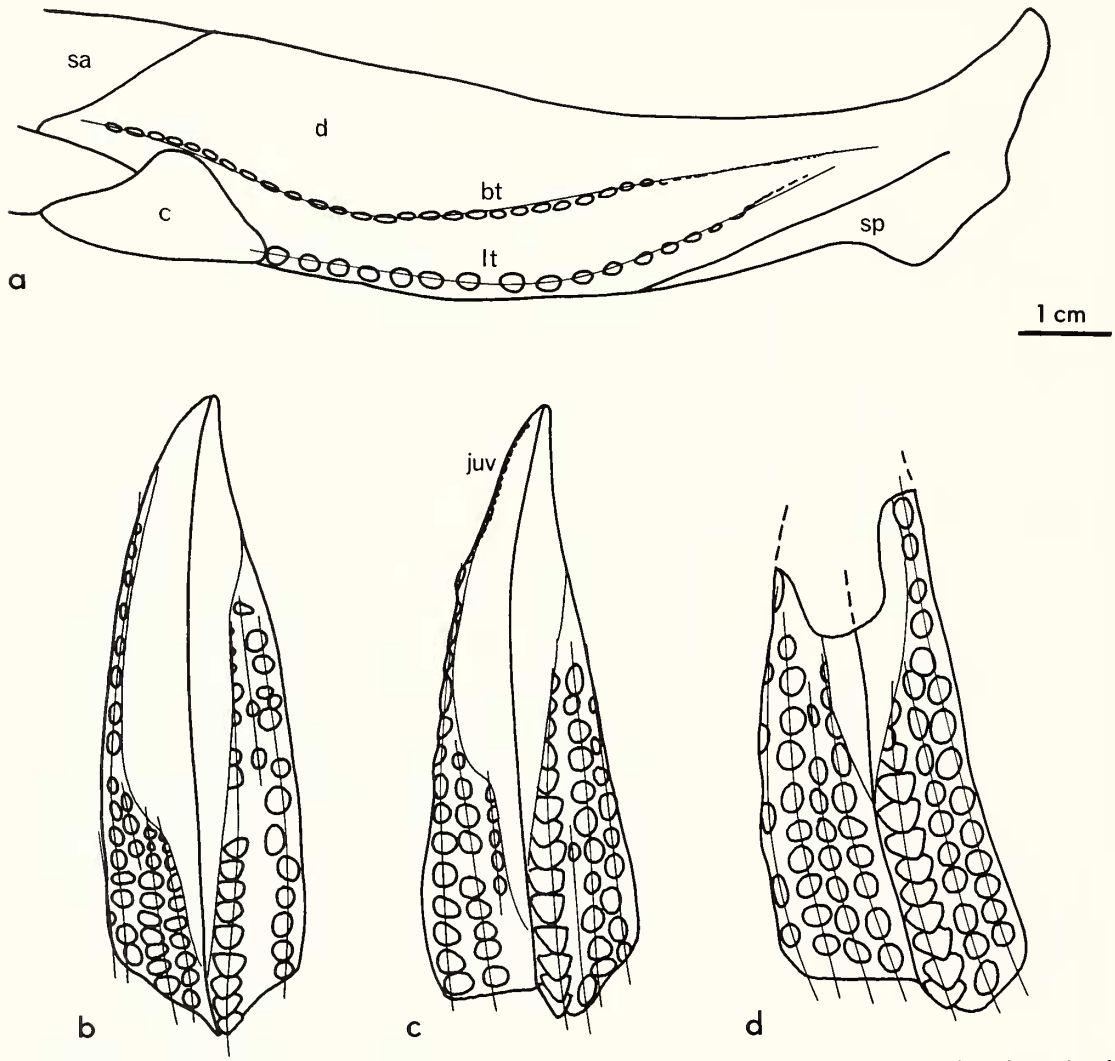
Evidence that rhynchosaurs added teeth posteriorly includes variation in tooth size, wear patterns, state of the pulp chamber, and growth of the tooth plate. The anterior teeth, when preserved, are tiny. One specimen of *Hyperodapedon gordoni* (NUGD B) shows ten to fifteen small teeth (diameter < 1 mm) on the medial edge which are sharply set off from those following behind (diameter 2–3 mm) (text-fig. 15*c*). These are probably equivalent to the remnant hatchling dentition of *Sphenodon* (Robinson 1976). Teeth initiated subsequently are of roughly equal size throughout life. The wear patterns clearly show the parts of the jaws that were in occlusion at death, and posterior teeth are unworn, which suggests that they had erupted last. The most posterior tooth in a longitudinal row may be very small, and probably barely erupted. In some specimens of *Stenaulorhynchus*, the most posterior tooth in certain Zahnreihen is missing, presumably since it failed to become ankylosed before the animal died (text-figs. 7*j*, 14*a*, *b*, *g*). Chatterjee (1974, p. 234) noted the same feature in *H. huxleyi*. Posterior teeth have open apical foramina and the occlusion of the root canal by deposition of secondary dentine may be followed in an irregular sequence along a Zahnreihe from the back of the jaw forwards (e.g. text-figs. 2, 10).

The maxillary tooth-plate at least grew by the addition of bone in successive layers. In *H. huxleyi*, the bone layers may be seen running diagonally upwards and forwards in a side view of the tooth-plate, and each layer is associated with a transverse row of teeth (Chatterjee 1974, pp. 232–233). This has the effect of lengthening and thickening the tooth-plate, and of making the front portion curve more and more upwards. Ricqlès and Bolt (1983, p. 11) noted 'strand lines' in the dentary of *Captorhinus* which they interpreted as indicating successive bursts of growth by posterior addition of



TEXT-FIG. 14. Patterns of teeth in the jaws of *Stenaulorhynchus*: dentary (*a*) and maxilla (*b–g*). The arrows indicate the anterior ends of each specimen. Zahnreihen are suggested and tooth form is coded. *a*, left dentary (BM(NH) R9273) in dorsal and medial views (cf. text-fig. 7*i*, *j*); *b*, left maxilla (BM(NH) R9279) in medial and ventral views (cf. text-fig. 7*a*, *b*); *c*, left maxilla (CUMZ T993) in medial and ventral views (cf. text-fig. 7*c*); *d*, left maxilla (BM(NH) R9275) in medial view; *e*, right maxilla (CUMZ T992) in medial and ventral views; *f*, right maxilla (CUMZ T1138) in medial and ventral views (cf. text-fig. 7*f*, *g*); *g*, right maxilla (BM(NH) R9281) in medial and ventral views (cf. text-fig. 7*d*, *e*).

bone. Similar indications of appositional growth may be seen in maxillae of *Stenaulorhynchus*, and the extensive 'migration' of blood-vessels through the bone confirms this (Pl. 68, fig. 1). The vessels all migrate up and backwards in order to maintain their correct relative positions as bone is added behind, below, and above. Further evidence for the growth directions of the jaws is seen in the clear orientation of vascular canals in the bone. In section, these run up and backwards in the dentary of *Hyperodapedon* (text-fig. 4*d*) and in the maxilla of *Stenaulorhynchus* (text-fig. 10), which indicates backwards and dorsal growth.



TEXT-FIG. 15. Patterns of teeth in the jaws of *Hyperodapedon gordoni*: dentary (*a*) and maxilla (*b–d*) in occlusal views. Zahnreihen are tentatively indicated: *a*, left dentary (NUGD B); *b*, left maxilla (NUGD A); *c*, left maxilla (NUGD B); *d*, left maxilla (EM 1926.6). In the maxillae, the areas of wear on either side of the groove are left blank and outlined. 'Juvenile' teeth (< 1 mm diameter) may be seen at the front of the maxilla of NUGD B (*c*). Abbreviations: bt, buccal teeth; c, coronoid; d, dentary; juv, juvenile teeth; lt, lingual teeth; sa, surangular; sp, splenial.

Dental lamina

The dental lamina in the dentary of *Stenaulorhynchus* probably lay in the marked U-shaped groove between the back of the tooth-bearing area and the coronoid (text-figs. 7*h*, 9*c*). The dental lamina probably continued forward in a shallow depression which runs forward from here on the medial surface of the dentary below the lingual tooth rows. There is a similar clear groove between the coronoid and dentary in *Hyperodapedon* for the dental lamina, but no sign of an anterior continuation, which was not necessary (text-fig. 1*d*). The dental lamina in the maxilla of *Stenaulorhynchus* also appears to have been situated partly posteriorly in the sharp groove between maxilla and ectopterygoid, and partly medially. There is a clear notch and anteriorly running depression on the side of the maxilla, just above the lingual teeth (text-fig. 7*f*, *g*). In *Hyperodapedon*, again, the dental lamina probably lay only posteriorly in the V-shaped notch between maxilla and ectopterygoid (text-fig. 1*b*). Chatterjee (1974, pp. 234, 236) noted just the same features in *H. huxleyi*.

Erosion, resorption and anterior loss of teeth

Individual teeth commonly cause resorption in others, although there is no evidence in rhynchosaurs of tooth replacement from below with the associated resorption of old teeth. The patterns seem to be associated with the small movements of the ankylosed teeth relative to each other as a result of continuous growth and remodelling of the bone of the jaws. A similar effect of tooth 'crowding' and consequent erosion has been noted in *Captorhinus* (Bolt and DeMar 1975; Ricqlès and Bolt 1983).

The patterns of erosion appear to indicate the relative ages of the teeth involved. Younger, more recently implanted teeth generally cause erosion in older ones. In the dentary of *Hyperodapedon*, the lingual teeth appear to cause damage to the buccal teeth when they come into proximity (e.g. text-fig. 3*d*; Pl. 67, fig. 5). The active open root apices of buccal teeth may cause mutual erosion when they meet (text-fig. 6*a–c*). In the maxilla of *Stenaulorhynchus*, young open-rooted teeth 'squeeze' their older anterior neighbours (text-figs. 10, 12*b*). Similarly, young teeth belonging to high Zahnreihen grow down into, and erode, older teeth that belong to other Zahnreihen (text-figs. 11*a*, *b*, 12*c*; Pl. 68, fig. 3). Exactly the same effects are seen in the dentary of *Stenaulorhynchus* (text-figs. 9*a*, 11*f*, 12*h*, 14*a*). In general then, in becoming ankylosed, a tooth may excavate a space for itself in the jaw-bone and this may damage teeth of different Zahnreihen that are already implanted.

It has already been noted that anterior teeth in *Stenaulorhynchus* and *Hyperodapedon* are generally heavily worn and often reduced further by resorption. Large amounts of tooth material may be removed leaving the root apex ragged (e.g. Pl. 66, fig. 2; Pl. 68, fig. 4). Teeth are 'lost' anteriorly by a combination of wear of the crown in occlusion and resorption of the root. This 'drift' of teeth from the posterior/lingual portion of the jaw to the anterior/labial portion, where they are lost, is a result of bone growth and remodelling. When worn teeth 'swing' out of occlusion their roots are resorbed. This is very similar to the mechanism postulated by Ricqlès and Bolt (1983) in *Captorhinus*.

Model of tooth replacement in rhynchosaurs

Rhynchosaurs have several longitudinal rows of teeth (Zahnreihen) in each tooth-bearing jaw element (maxilla and dentary). Teeth are not replaced from below. During normal jaw growth, teeth are added posteriorly or posteriorly and lingually to each Zahnreihe. If the tooth-bearing bone becomes wide enough, additional Zahnreihen may be initiated. The addition of teeth appears to depend on the available area of dentigerous bone in the proximity of the dental lamina. Newly implanted teeth have widely open pulp chambers and small enamel caps. They swing into occlusion as the jaw-bones rotate relative to each other. This 'rotation' is slight and occurs to maintain an adequate occlusal surface between dentary and maxilla as the animal increases in size. In occlusion, the enamel tooth cap is soon lost and the tooth becomes flattened, and then dentine and bone are worn at the same rate. Secondary dentine gradually fills the pulp chamber. As the occlusal area moves back with further growth, the heavily worn anterior teeth swing out of occlusion. Their roots are largely resorbed and they are reduced in size. They are finally lost anteriorly or antero-labially. Throughout its life, a tooth may seem to move forwards through the jaw, as if on a conveyor belt, but

this effect is produced by relative growth of the jaw and remodelling rather than by 'drift' of teeth through the bone of the jaw.

The reality of the Zahnreihen is indicated by the simple observations of the relative ages of teeth in one longitudinal row: oldest at the front and youngest at the back. Further, the youngest Zahnreihe is located medially of the older ones. This is shown in a cross-section by the stages of development of individual teeth that belong to different Zahnreihen, and their mutual erosion effects: medially placed teeth cause erosion of their laterally placed neighbours. The former were clearly implanted after the latter.

FUNCTION OF THE RHYNCHOSAUR DENTITION

Many of the anatomical and histological features of the ankylothecodont rhynchosaur teeth may be understood by a comparison with living acrodont reptiles in which teeth are also not replaced from below, but are added posteriorly. Amongst living reptiles, acrodont teeth are seen in *Sphenodon* (Robinson 1976), and in two families of lizards, the Agamidae and the Chameleontidae. Such teeth must have a longer functional life than those of a typical polyphyodont reptile. The large agamid *Uromastix* displays various mechanisms that contribute to this (Throckmorton 1979): enamel and dentine layers are thickened; secondary dentine grows to fill the pulp chamber; a bony core in the pulp chamber facilitates its eventual obliteration; the jaw-bone is able to perform a shearing function once the teeth are completely worn away; the cancellous bone supporting posteriormost teeth changes to completely compact bone supporting anterior teeth; the teeth may move through the jaw-bones to remain in good occlusion.

Stenaulorhynchus and *Hyperodapedon* display a thick dentine layer and the slow obliteration of the pulp chamber by the growth of secondary dentine. However, the enamel layer is not well developed—it is little more than a cap on the crown and it is rapidly worn away. A bony core in the pulp chamber was not seen in *H. gordoni*, although Chatterjee (1974, p. 230) reported this feature in *H. huxleyi*. The loose bone noted above in the pulp chambers of some *Stenaulorhynchus* teeth may be an homologous structure. The bone of dentary and maxilla clearly performs the same function as the teeth and, in fact, most occlusion is between tooth and bone. Because of this, precise tooth–tooth occlusion and extensive remodelling of the bone was probably not necessary. The bone at the roots of the teeth of *Stenaulorhynchus* and *Hyperodapedon* is cancellous around the posterior 'active' teeth, and compact around the anterior teeth that have moved out of occlusion.

It has been suggested that rhynchosaurs ate plant material (Huene 1939; Romer 1963; Sill 1971*a*, *b*) or molluscs (Burckhardt 1900; Chatterjee 1969, 1974, 1980). In support of the latter view, Chatterjee (1974, 1980) has noted wear facets on teeth of *H. huxleyi* not caused by the opposing teeth, and the presence of molluscs in association with the Indian rhynchosaur.

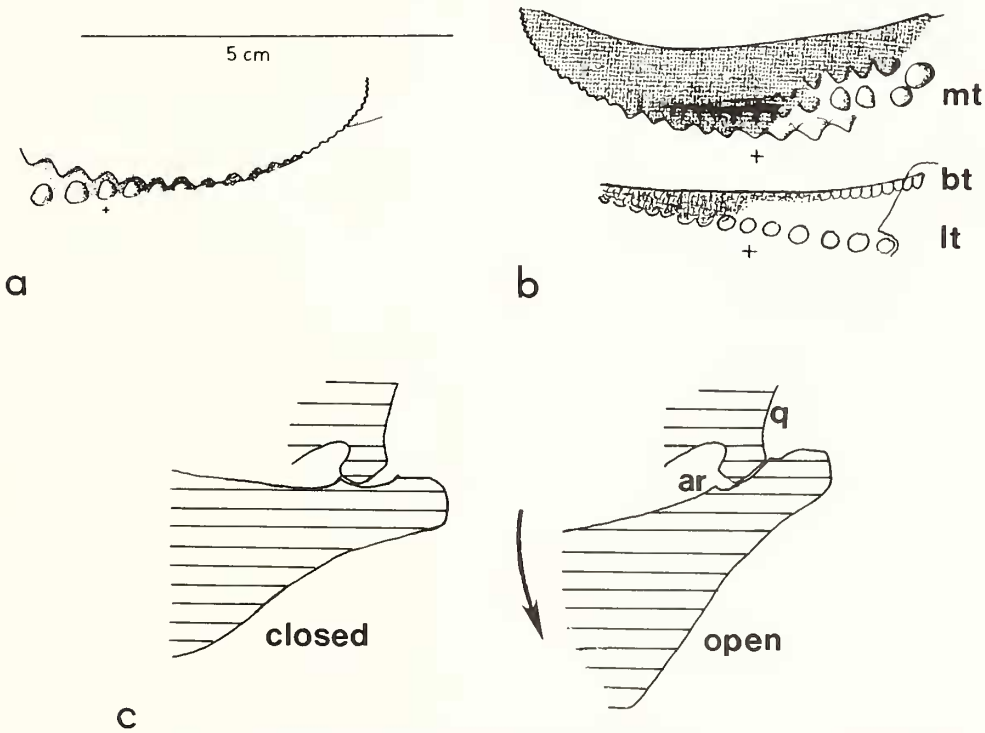
A detailed study of the teeth and jaws of *Hyperodapedon* and *Stenaulorhynchus* gives no evidence for mollusc-eating. The teeth are not polished and hard like those of chimaeras, stingrays, dipnoans, the extinct placodonts, and other animals that crush shells (Hildebrand 1974, p. 683). In fact, enamel is present only as a thin layer (Sill 1971*b*; Chatterjee 1974; Benton 1983*b*), and is usually worn from the exposed portions of occluding teeth. The tooth shape and arrangement are also different from those of living mulluscivores. Rhynchosaur teeth were sharp and conical rather than broad and flattened. The deep groove in the maxilla and the blade-like dentary are also quite different from the usual flattened pavement-like pounding-board dentition of a shell-crusher.

Wear patterns on the teeth and the jaw articulation of *Hyperodapedon* indicate a precision-shear biting action—that is, an accurate scissor-like cutting stroke with no back-and-forwards movement. Wear is clearly indicated in smooth arc-shaped areas and flattened tooth crowns in the middle and anterior parts of the maxilla and dentary (text-fig. 16*a*). There are several clear pits on the medial side of the maxillary tooth-plate groove for the lingual teeth of the dentary (text-fig. 16*b*), and these show that no longitudinal sliding of the jaws could have occurred. Posterior teeth do not come into contact and they often have very sharp points. The jaw articulation is between a heavy quadrate condyle and a cup-like glenoid facet on the articular of the lower jaw. Each facet is divided into two portions set at

a slight angle to each other. When models of the elements are placed together, it can be shown that the contact rocks back and forwards on the facets without sliding (text-fig. 16*c*). An anterior and posterior lip on the articular further prevent any back-and-forwards motion of the lower jaw, contrary to the findings of Sill (1971*b*) in *Scaphonyx*. The jaw mechanics of *Hyperodapedon* have been described in more detail elsewhere (Benton 1983*b*).

All of these features of the jaws and teeth of rhynchosaurs again suggest an appropriate modern functional analogue in the agamid lizard *Uromastix* (Robinson 1976; Throckmorton 1976, 1979). *Uromastix* is herbivorous and it efficiently crops leaves, flowers, shoots, and fruit of a wide variety of plants, but does not masticate the food. Unlike insectivorous and carnivorous agamids, the teeth of *Uromastix* are expanded back and forwards to form a nearly continuous cutting edge, the jaw action is scissor-like and both tooth and jaw-bone can perform the cutting function.

Further evidence in favour of an herbivorous diet for *Hyperodapedon* and other 'typical' rhynchosaurs is the barrel-shaped body (to accommodate a large gut for the slow digestion of vegetable material), the large numbers of these animals present in their respective faunas, and the



TEXT-FIG. 16. Tooth wear and jaw action in *Hyperodapedon gordoni*. *a*, close-up view of the jaws closed in medial view, with maxillary teeth (above) overhanging the lower jaw buccal teeth and most of the lingual teeth (cf. text-fig. 1). *b*, lateral view of the medial half of the maxillary tooth plate (above) and medial view of part of the dentary (reversed) so that corresponding teeth and wear cavities may be matched: the lingual tooth marked '+' fits into the pit marked '+' on the maxilla; areas of wear are patterned; posterior teeth of all series are unworn. *c*, jaw opening movement at the articulation in diagrammatic longitudinal section; there are two articulating fields on both articular and quadrate, and the contact changes to the posterior fields when the jaw opens. Abbreviations: ar, articular; bt, buccal teeth; lt, lingual teeth; mt, maxillary teeth; q, quadrate.

general rarity of associated fossil mollusc shells. Several rhynchosaurs have been found associated with fragmentary plants, and the diet probably consisted of leaves, stems, fruit, and seeds of seed-ferns, conifers, ginkgos, equisetaleans, and ferns. Rhynchosaurs could not grind up plant food, but they may have been able to 'ruminate'. Food could be gathered by the use of the beak-like premaxillae, manipulated with the large tongue, and efficiently cropped and sliced by the powerful jaws. The hindlimb was strong and apparently adapted for scratch-digging (Benton 1983*b*), so that *Hyperodapedon* could dig up edible tubers and roots.

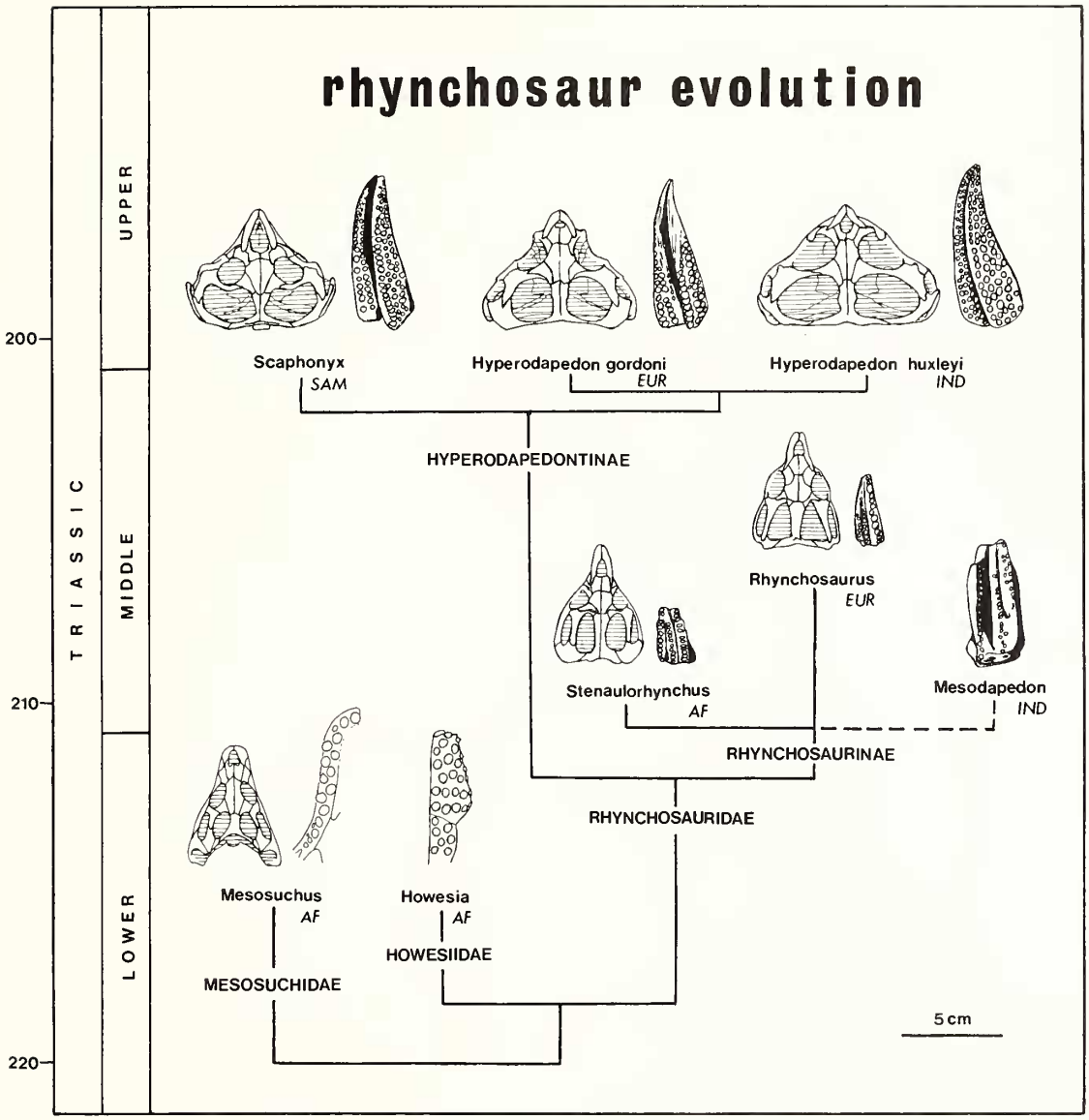
EVOLUTION OF THE RHYNCHOSAUR DENTITION

The origin of the rhynchosaurs (early–late Triassic) is uncertain. They clearly belong within the Subclass Diapsida and within an archosauromorph assemblage, which also includes prolacertiforms (early–late Triassic) and archosaurs (latest Permian–present day) (Benton 1983*b*, 1984). They are not closely related to *Sphenodon*, as has been assumed hitherto by most authors. Romer (1956) suggested that rhynchosaurs were derived from a generalized 'eosuchian' ancestor such as *Youngina* from the late Permian of South Africa. However, *Youngina* is a lepidosauromorph diapsid on the basis of its specialized intervertebral articulations, single-headed dorsal ribs, and probable fused bony sternum, and it has no particular relationship to rhynchosaurs. Carroll (1976) redescribed *Noteosuchus* from the earliest Triassic *Lystrosaurus* Assemblage Zone of South Africa as the oldest-known rhynchosaur on the basis of numerous characters shared with the slightly later rhynchosaurs *Mesosuchus* and *Howesia*. However, these are shared also with prolacertiforms and early thecodontians, and *Noteosuchus* must be classified as 'Archosauromorpha *incertae sedis*' at present (Benton, 1983*b*). Diagnostic portions such as the forelimb and the skull have not been found.

The remaining rhynchosaurs have been classified as follows (text-fig. 17) on the basis of shared derived characters of the skull and skeleton (Benton 1984):

Order Rhynchosauria Osborn 1903 (Gervais 1859)
- Suborder Mesosuchidia Haughton 1924
  - Family Mesosuchidae Haughton 1924
    - *Mesosuchus* (*Kannemeyeria* Assemblage Zone (*Cynognathus* Zone), South Africa; lower Triassic)
- Suborder Rhynchosauroidea Nopcsa 1928
  - Family Howesiidae Watson 1917
    - *Howesia* (*Kannemeyeria* Assemblage Zone (*Cynognathus* Zone), South Africa; lower Triassic)
  - Family Rhynchosauridae Huxley 1887
    - Subfamily Rhynchosaurinae Nopcsa 1923
      - *Rhynchosaurus* (Helsby Sandstone Formation, Tarporley Siltstone Formation, Bromsgrove Sandstone Formation, Otter Sandstone Formation, England; middle Triassic)
      - *Mesodapedon* (Yerrapalli Formation, India; middle Triassic)
      - *Stenaulorhynchus* (Manda Formation, Tanzania; middle Triassic)
    - Subfamily Hyperodapedontinae Chatterjee 1969
      - *Hyperodapedon* (Lossiemouth Sandstone Formation, Scotland and Maleri Formation, India; upper Triassic)
      - *Scaphonyx* (Santa Maria Formation, Brazil and Ischigualasto Formation, Argentina; upper Triassic)
      - '*Supradapedon*' (Tanzania; ?upper Triassic)
      - Undescribed genera (Wolfville Sandstone, Nova Scotia and Dockum Group, Texas; upper Triassic)

Mesosuchus has rhynchosaur-like features of the skull and skeleton, but the dentition is rather different. The teeth on maxilla and dentary appear to have a zigzag arrangement (Malan 1963). *Howesia* has multiple rows of ankylothecodont teeth with lingual and posterior addition, but



TEXT-FIG. 17. Evolution of the rhynchosaurs. A dorsal view of each skull is given, when known (all drawn to a standard length), and a left maxillary tooth-plate (see 5 cm scale) is shown for each genus. The relationships are based on a detailed phenetic and cladistic study of all genera (Benton 1983*b*). The occurrence in time and space (AF, Africa; EUR, Europe; IND, India; SAM, South America) is indicated for each genus. The early Triassic *Noteosuchus* is omitted since its skull is not known and its relationships are uncertain. '*Supradapedon*' (a large maxillary tooth-plate from the ?late Triassic of Tanzania; Chatterjee 1980) and the undescribed North American rhynchosaurs are also omitted. Sketches after Woodward (1907), Huene (1938), Malan (1963), Romer (1966), Chatterjee (1974, 1980), and Benton (1983*b*).

apparently no 'groove and blade' mechanism of the jaws. In many respects, its dentition resembles that of advanced captorhinomorphs (c.f. text-fig. 13).

The middle Triassic rhynchosaurs form a distinct group. Their maxillae show two grooves and one or more tooth rows between the grooves. There are teeth on the lingual face of the maxillae in all three forms, but these run over the jaw edge on to the occlusal surface. The dentary has tooth rows elevated on two ridges that fit into the maxillary grooves. In both dentigerous elements, the teeth are organized into longitudinal Zahnreihen, clearly analogous with those of *Howesia* and captorhinomorphs.

The late Triassic rhynchosaurs are all very similar in characters of the skull and skeleton, and they form another natural group. The maxilla has one groove and the dentary has a single sharp ridge that fits neatly into the groove. Maxillary teeth are organized into longitudinal rows on the occlusal surface with none on the lingual side. The teeth on the dentary form two clearly separate rows—one on the apex (the buccal teeth) and one lower down on the medial face (the lingual teeth). The latter row engages with teeth on the medial portion of the occlusal surface of the maxilla. The South American form *Scaphonyx* generally lacks lingual teeth on the dentary, although Contreras (1982) has recently described a rhynchosaur from the lower Ischigualasto Formation of Argentina which has well-developed lingual teeth.

The dentition of the late Triassic group of rhynchosaurs can be regarded as a modification and simplification of that of the middle Triassic group (text-fig. 17): there is a single groove in the maxilla, and the tooth rows of the maxilla are all on the occlusal surface (and the dental lamina is probably entirely posterior in position), and the number of tooth rows on the dentary reduces.

Chatterjee (1980) has recently proposed a classification of rhynchosaurs which differs from that given above in which he associates the European and African forms (*Stenaulorhynchus*, *Rhynchosaurus*, *Hyperodapedon gordoni*, '*Supradapedon*') in one subfamily, and the American and Indian forms (*Mesodapedon*, *Scaphonyx*, *H. huxleyi*, North American forms) in another. This classification was based on a single character of the arrangement of the teeth on the maxillary tooth-plate. I believe that this character is not consistently present and the classification is therefore unworkable. The weight of evidence is very much against Chatterjee's (1980) classification (see Benton (1983*b*) for fuller details).

CONCLUSIONS

1. The dentition of rhynchosaurs is of great taxonomic importance since it has been used as evidence that rhynchosaurs are closely related to *Sphenodon*. However, the dentitions are quite different: rhynchosaurs do *not* have acrodont teeth, the groove is on the maxilla only (not between maxilla and palatine, as in *Sphenodon*), and the jaw action is quite different (no propalinal movement, as is seen in *Sphenodon*).

2. The dentition of rhynchosaurs is highly unusual in terms of anatomy and development. Many parallels have been discovered with the acrodont teeth of some living lizards and with the dentition of fossil captorhinomorphs. In all of these groups, teeth are not replaced from below, as is the case in typical polyphyodont reptiles. There is clear evidence here for the reality of Zahnreihen as a feature of the pattern of the dentition, and in all cases the history of a Zahnreihe may be followed from newly ankylosed, unworn teeth at the back, through actively remodelling areas which are in occlusion, to old heavily worn and largely resorbed teeth at the front. The bone of the jaws grew mainly at the back of the tooth rows, and teeth appeared posteriorly as the area of dentigerous bone increased. There is no evidence for subsequent 'drift' of the teeth through the bone, other than minor movements produced by normal remodelling of the jaws while in occlusion.

3. Problems for further study include a detailed examination of the teeth of the early rhynchosaurs *Mesosuchus* and *Howesia* in the hope that this might shed some light on the origin of the typical multiple-rowed dentitions of later forms. It must be assumed that the ancestors had a single-row dentition, but nothing is known of that. The specific adaptations of the rhynchosaur feeding mechanism are also a matter for further work. Rhynchosaurs were very important animals in the Triassic, and yet their ecological role is still a matter of debate (Benton 1983*a*, *b*). Further study

should also be devoted to the problems of tooth maintenance and replacement in non-polyphyodont reptiles and the question of the evolutionary advantages or disadvantages of such a system. Finally, multiple-row reptile dentitions, which effectively 'freeze' a considerable time span of tooth pattern development, should shed further light on the problem of the reality, or non-reality, of Zahnreihen as descriptive units, if not as developmental indicators.

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